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# A comparison of temperature regulation in neonatal and adult hispid cotton rats, *Sigmodon hispidus texianus*, from southern Texas and northern Kansas

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A COMPARISON OF TEMPERATURE REGULATION IN NEONATAL AND  
ADULT HISPID COTTON RATS, SIGMODON HISPIDUS TEXIANUS, FROM  
SOUTHERN TEXAS AND NORTHERN KANSAS

*Iowa State University*

PH.D.

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A comparison of temperature regulation in neonatal  
and adult hispid cotton rats, Sigmodon hispidus texianus,  
from southern Texas and northern Kansas

by

Stephen Henderson Scheck

A Dissertation Submitted to the  
Graduate Faculty in Partial Fulfillment of the  
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Iowa State University  
Ames, Iowa

1980

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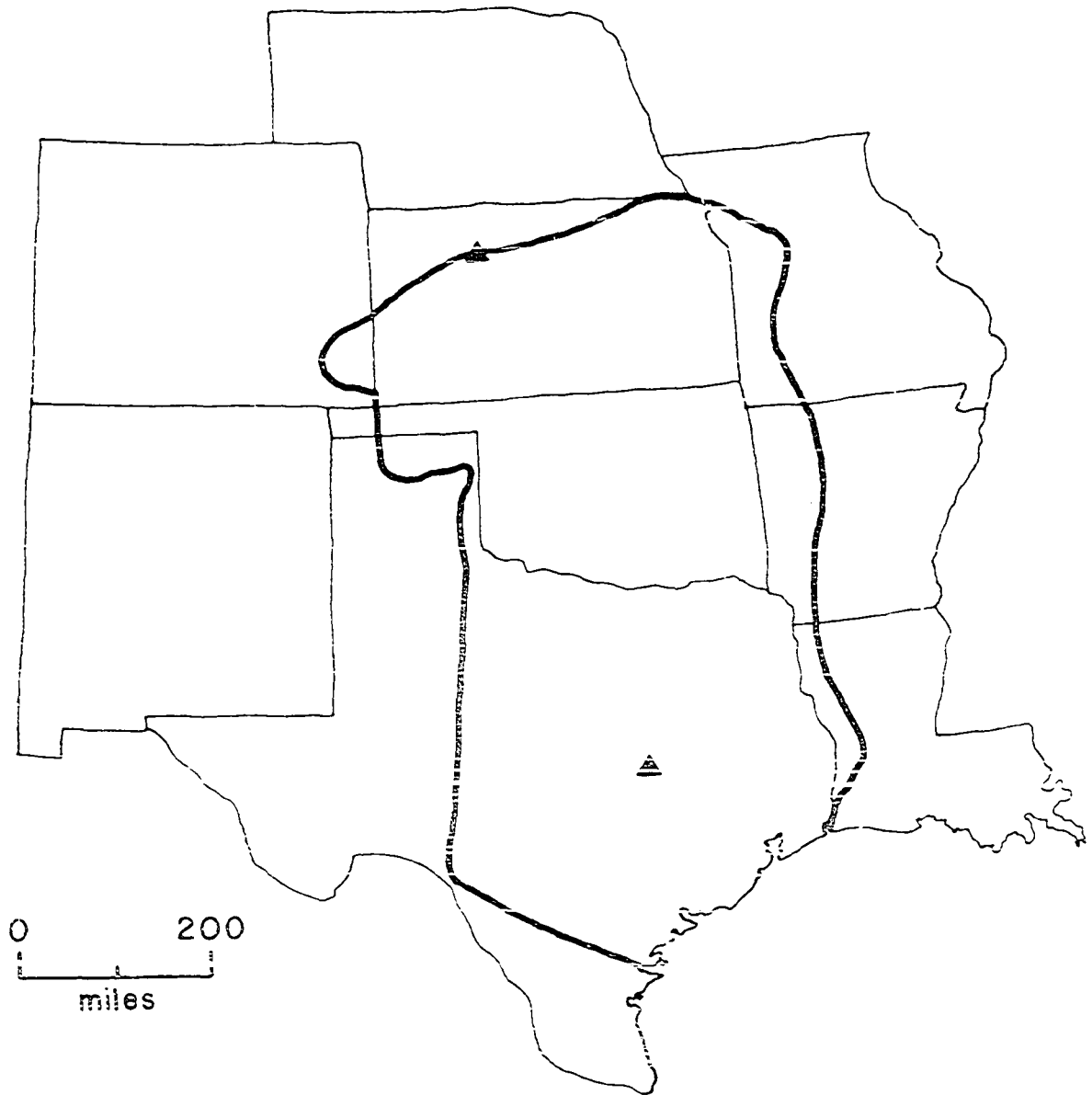
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## INTRODUCTION

The hispid cotton rat, Sigmodon hispidus texianus (Audubon and Bachman), is an herbivorous species which generally inhabits mesic areas (Martin, 1960; Fleharty and Mares, 1973). The range of S. h. texianus extends from south-central Texas northward to extreme northern Kansas and from western Missouri, Arkansas and Louisiana westward to eastern Colorado and the Oklahoma and Texas panhandles (Hall and Kelson, 1959) (Fig. 1).

The northward dispersal of the hispid cotton rat into more temperate regions has received considerable documentation (Bailey, 1902; Hibbard, 1933, 1944; Rinker, 1942b; Cockrum, 1948, 1952; Hall, 1955; Jones, 1960, 1964; Genoways and Schlitter, 1966; Liesveld and Fiala, 1977; Carey, 1978). Cockrum (1948) presents a detailed summary of the northward advancement of this species within Kansas (Fig. 2). The genus Sigmodon is subtropical in origin and for the most part, distribution (Hooper, 1949; Hibbard, 1960); consequently, animals at the northern periphery are at times subjected to extremely inhospitable environments. However, the hispid cotton rat has continued to extend its range northward. Indeed, captures of this species have been reported for extreme south-central (Genoways and Schlitter, 1966) and south-eastern (Liesveld and Fiala, 1977) Nebraska, respectively. It is unlikely that this movement northward through Kansas (within the last century) can be linked to general climatic changes on the Great Plains since the climatic regime in this region of North America has not changed as abruptly as the northern movement of the hispid cotton rat

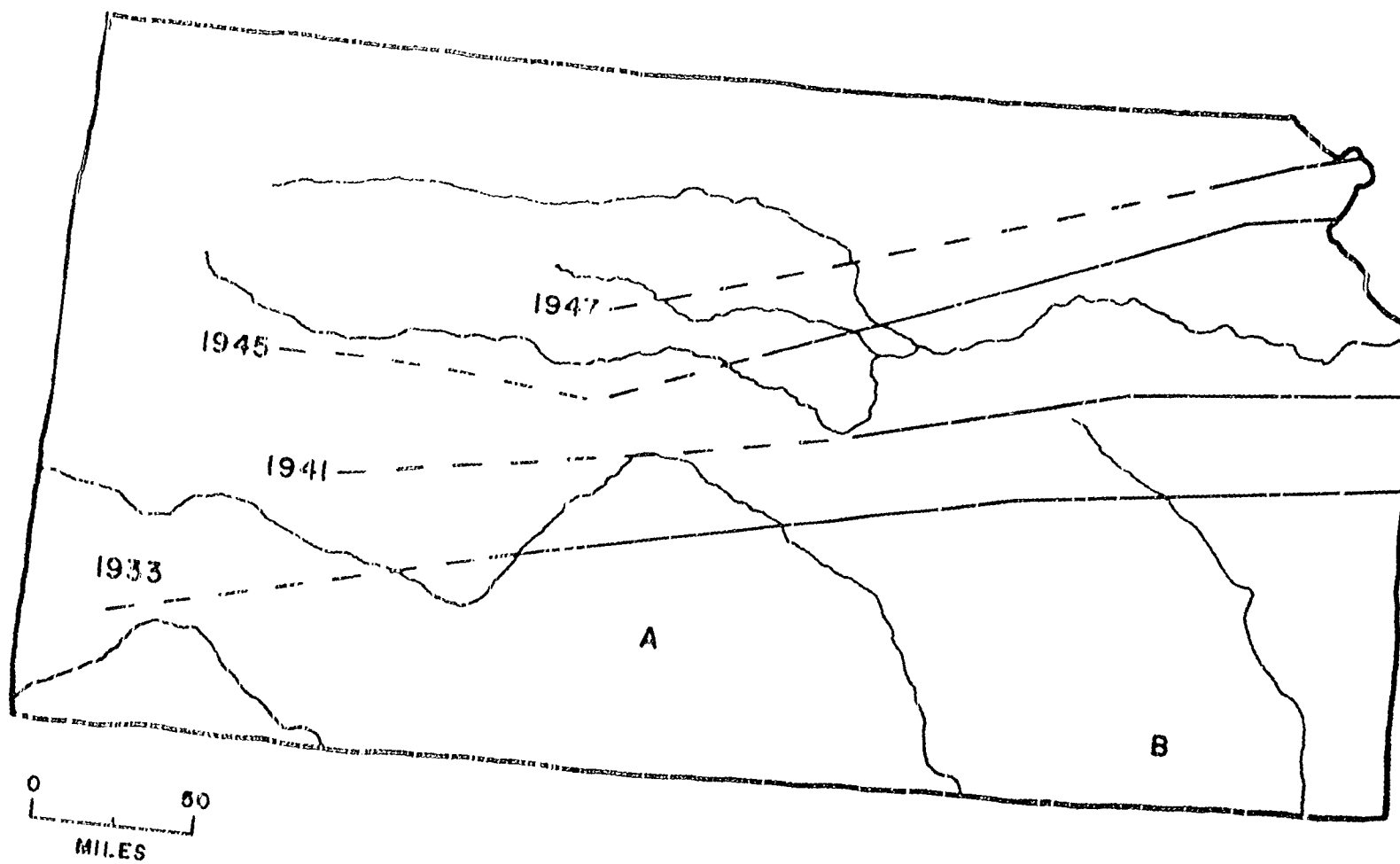
Fig. 1. Map of central and south-central United States indicating the distribution of Sigmodon hispidus texianus (according to Hall and Kelson, 1959). Solid triangles represent localities from which Texas and Kansas animals were procured.



*Sigmodon hispidus texianus*



Fig. 2. Map of Kansas showing northern boundaries of Sigmodon hispidus texianus from 1933 to 1947. Solid lines represent known limits of the distribution. Dashed lines represent probable limits of the distribution. Localities A and B represent the 1st and 2nd confirmed captures of S. h. texianus in Kansas (1902 and 1904, respectively). Map is adapted from Cockrum (1948).



(Hoffmann and Jones, 1970; Fleharty et al., 1972).

In order to better understand this northward movement, numerous studies have examined various aspects of the life history of the hispid cotton rat. Most notable are those studies which have directed attention toward examination of the structure/dynamics of cotton rat populations (Calhoun, 1945; Odum, 1955; Goertz, 1964; Chipman, 1966; Haines, 1971; Fleharty et al., 1972; Fleharty and Mares, 1973; Joule and Cameron, 1974; Bigler and Jenkins, 1975) and those which have looked at reproductive strategies of the cotton rat (Rinker, 1942a; Meyer and Meyer, 1944; Goertz, 1965a,b; Kilgore, 1970; Bowdre, 1971; Haines, 1971; Randolph et al., 1977; McCleughan and Gaines, 1978; Dowler and Engstrom, 1979). Especially pertinent to the understanding of this northward movement are studies which have addressed the differences in the biology of the cotton rat at different latitudes (Kilgore, 1970; Bowdre, 1971; McCleughan and Gaines, 1978) or during different seasons of the year (Goertz, 1964, 1965a,b; Chipman, 1965, 1966; Haines, 1971; Fleharty et al., 1972; Fleharty et al., 1973; Fleharty and Choate, 1973; French et al., 1976; McClenaghan and Gaines, 1978).

Findings reported in the aforementioned studies have indicated that the hispid cotton rat has undergone changes in its behavior and physiology in order to cope with the climatic regimes of the more northern latitudes (37-40° N lat.). Hispid cotton rats at all temperate latitudes tend to exhibit a seasonality in population densities with periods of abundance and scarcity occurring during the fall and late winter-early spring, respectively (Komarek, 1937; Odum, 1955; Goertz,

1964; Fleharty et al., 1972). In addition, cyclic changes in population densities may appear from year to year (Odum, 1955; Haines, 1971), every 4-5 years (Komarek, 1937) or approximately every 10 years (Schendel, 1940; Cockrum 1952; Martin, 1960; Dunaway and Kaye, 1961; Haines, 1963). Populations may also experience greatly reduced numbers or local extinction ("crash") during severe winters (Howard, 1951; Odum, 1955; Dunaway and Kaye, 1961; Fleharty et al., 1972). It has been hypothesized that the stress imposed upon the animals by exposure to severe cold weather is the primary cause for population declines during winter (Hoffmann and Jones, 1970; Goertz, 1964; Fleharty et al., 1973). Fleharty et al. (1972) suggested that such cold weather stress probably is the major factor in determination of the northern boundary for the distribution of this subspecies.

Strategies noted in S. hispidus to cope with exposure to cold weather at the northern regions of its distribution include:

- 1) increased lipid deposition during the fall (Fleharty et al., 1973; Fleharty and Choate, 1973; Cameron et al., 1979b)
- 2) utilization during winter of heavily insulated surface nests (Gaertner, 1968; Shump, 1978) or subterranean nests (Schendel, 1940; Goodpaster and Hoffmeister, 1952; Baar et al., 1975)
- 3) huddling (Schendel, 1940; Dunaway and Kaye, 1961; Wiegert and Mayenschein, 1966) which results in a reduction of metabolic heat loss to the environment (Pearson, 1960)

- 4) restriction of movements to areas with dense stands of vegetation which yield a more hospitable microclimate (more so with a canopy of snow) and a more abundant supply of food than areas with less vegetative cover (Goertz, 1964; Fleharty and Mares, 1973)
  - 5) inactivity throughout periods of extreme cold (Howard, 1951; Goertz, 1964; Baar et al., 1975); however, unless sufficient body lipid is available, protracted periods of inactivity (animals remain in nests) may lead to "cold weather starvation" (Howard, 1951) since cotton rats are not known to store food (Schendel, 1940)
  - 6) suppression of secondary production (i.e., growth and reproduction) during severe periods of cold so that utilization of body energy reserves and energy intake is solely for individual survival (Fleharty and Choate, 1973; McCleaghan and Gaines, 1978)
- and 7) most likely, general acclimitization changes occur as have been reported for other mammalian species; e.g., increased thickness of the pelage (Heroux et al., 1959; Heroux, 1962; Hart et al., 1965; Hart, 1971), increased basal metabolic rate (Hart, 1971; Bradley et al., 1975; Hinds, 1977; Wunder et al., 1977) and haemoconcentration (Lee and Brown, 1970; Maclean and Lee, 1973)

These factors undoubtedly have contributed to the success of the northward movement of the cotton rat through Kansas (Fig. 2).

Members of one geographically distinct population (population A) may exhibit characteristics (life strategies) that are not exhibited by members of another (population B). If members of population A exhibit a given characteristic and members of population B do not, one may not conclude that members of population B are incapable of exhibiting the given characteristic (i.e., are not genetically capable to exhibit the characteristic). A case in point: hispid cotton rats in Kansas (population A) construct heavily insulated nests whereas hispid cotton rats in Florida (population B) do not. The differences in degree of insulation of the nest are directly correlated to the ambient temperature; the cooler the mean ambient temperature, the more heavily insulated the nest (Shump, 1978). However, if rats from both Kansas and Florida are maintained in the laboratory under environmental conditions that are reversed (i.e., rats from Florida exposed to "Kansas-like" temperatures and rats from Kansas exposed to "Florida-like" temperatures), the animals will construct the appropriately insulated nests for the ambient temperatures to which they are exposed (Shump, 1978). Much of the literature on differences in the life histories of geographically distinct populations of S. hispidus has been generated from studies in the field. Therefore, the question of whether acclimatization or genetic adaptation is responsible for a given characteristic exhibited by a particular population cannot be answered. [See Folk (1974) for definitions of terms.]

Consequently, different physiological and behavioral patterns exhibited by S. h. texianus (at varying latitudes) in response to

winter conditions cannot be positively implicated as effects due either to acclimitization or to genetic adaptation. If genetic (phylogenetic) adaptation is involved, thereby evolving increasingly cold-tolerant animals at the northern perimeters of the range, the relatively sudden and rapid movement northward of this subspecies through Kansas would not seem surprising (Fig. 2).

In order to test for the possibility of phylogenetic adaptation for increased cold-tolerance in animals from the northern regions of the range as compared to animals from the southern regions of the range, a basic physiological process was selected: metabolism/thermoregulation. The ability (effectiveness) to thermoregulate was selected because of its crucial importance to an individual's response to exposure to cold. Animals that are adapted for an increased ability to regulate their body temperature at low ambient temperatures (in addition to acclimitization changes for winter), can withstand cold exposure, at least for short periods of time, more successfully than animals who are not equally adapted. Such an advantage could play a significant role in winter survival, especially when considering the alternatives of undergoing "cold weather starvation" (Howard, 1951) or foraging for food during extremely cold temperatures. This potential advantage, however, necessitates that such foraging for food produces a net energy gain, i.e., the animal collects more energy via food consumed and assimilated than is expended during the foraging episode.

Previous studies have looked into the possibility of temperature adaptation in homeotherms with mixed results. Scholander et al., (1950)

and Enger (1957) found no adaptive abilities of metabolic rates of arctic and tropical mammals and birds. Hayward (1965) also found no adaptive abilities in six geographic races of Peromyscus. Cook and Hannon (1954) found significantly different standard metabolic rates in three geographic races of Peromyscus at different altitudes but attributed the differences to different levels of oxygen in the animals' temperaments.

Contrary to the above evidence of nonadaptive metabolic rates, other authors have observed adaptive differences in metabolic rates. Differences in metabolic rates have been shown in six species of Heteromyids (Dawson, 1955; Bartholomew and MacMillan, 1961; Carpenter, 1966; McNab, 1979), five species of Peromyscus (McNab and Morrison, 1963) and six species of Spermophilus (Citellus) (Hudson et al., 1972; Hudson and Deavers, 1973). However, even in these cases, the adaptations exhibited by the animals seem to be more closely related to a need for reduction of insensible water loss (Murie, 1961) rather than to a response to cold stress.

Bowers (1971) examined resting metabolic rates in eleven subspecies (5 species) of Sigmodon that were acclimated in the laboratory (including S. h. texianus) for possible phylogenetic adaptations. Results from Bower's (1971) study indicate that two groups (representing 2 species) have resting metabolic rates significantly different from each other and from the nine other groups. However, as previously discussed, the differences are thought to be due to the extremely xeric



or mesic environments in which the two species live and consequently the need, or lack thereof, for water conservation.

Some studies showing geographic variation in metabolic rates of rodents have been carried out by Russian scientists (Hart, 1971). The most encouraging results (i.e., supportive of phylogenetic adaptation of metabolic rate to cold) have been obtained by Kalabukhov and Ladygina (in Hart, 1971). These scientists maintained Apodemus flavicollis from a northern race (Kharkov region) and a more southern race (Crimea region) in captivity over several generations. Northern animals, several generations removed from the wild, still maintained lower metabolic rates at low ambient temperatures (as did their wild-caught ancestors) than did their southern counterparts.

It becomes apparent that there is a paucity of clearly defined examples of phylogenetic adaptation of metabolic rate to cold. Weathers (1979) has presented data which indicate a strong probability of phylogenetic adaptation for increased standard metabolic rates in birds at more northern latitudes when compared to similar birds at more southern latitudes.

If one assumes that phylogenetic adaptation of metabolic rate to cold does exist in S. h. texianus at the northern periphery of its range, it would be of interest to know if such an adaptation is functional at birth or if it is expressed only in more matured individuals. Therefore, the purpose of my dissertation research is to reexamine the concept of phylogenetic adaptation of metabolic rates to cold in both young and adult mammals. The hispid cotton rat,

S. h. texianus is used in this study due to the unique distributional status that exists within this subspecies; as has previously been discussed at length.

#### Thermoregulation in Neonates

Previous work on the thermoregulatory ability of neonatal hispid cotton rats is limited to one study (Randolph et al., 1977). In this study, the oxygen consumption of groups of 4 animals, from birth to adulthood, was determined while animals were exposed to an ambient temperature of 20 C. It was found that after day 40, oxygen consumption decreased until weights over 95 grams were reached, approximately 50-100 days of age (Meyer and Meyer, 1944). Randolph et al. (1977) did not test neonates individually at any ambient temperature or in litters at ambient temperatures other than 20 C. Many studies on other species, however, have examined the thermoregulatory abilities of individual neonates and litters exposed to various ambient temperatures.

Generally, three methods have been utilized for estimation of the thermoregulatory ability of neonates: 1) determination of cooling curves, 2) measurement of oxygen consumption and 3) a combination of the previous two. Cooling curves have been used to evaluate the thermoregulatory ability of neonates in many of the studies on neonatal thermoregulation (Morrison and Petajan, 1962; Lagerspetz, 1962; Hissa, 1964, 1968; Hissa and Lagerspetz, 1964; McManus, 1971; Maxwell and Morton, 1975; Goodrich, 1977; Olmstead et al., 1979; Sales and Skinner, 1979). Basically, this method involves placement of a thermocouple

rectally, subcutaneously or on the surface of the body. The animal is then exposed to a constant low ambient temperature and the rate of fall in body temperature is plotted against time of exposure. As an animal's thermoregulatory ability increases with age/weight, the rate of fall in body temperature decreases when exposed to low ambient temperatures. Eventually, little or no fall in body temperature is noted at which time the animal is said to have achieved homeothermy (the ability to maintain stable high body temperatures at varying ambient temperature). With the use of cooling curves, although determination of when complete ability to thermoregulate can be made, the ability an animal possesses for endothermy (internal production of heat that allows high and stable body temperatures at varying ambient temperature) cannot be determined.

The second method for estimation of thermoregulatory ability, measurement of oxygen consumption, does permit quantification of the capability for endothermy possessed by the neonate. Oxygen consumption is directly correlated to caloric output of an animal and therefore, is a good index of internal heat generation. Numerous studies have utilized the oxygen consumption method for estimation of neonatal thermoregulatory ability (Fitzgerald, 1953; Taylor, 1960; Cassin, 1963; Dawes and Mestyan, 1963; Hull and Segall, 1965a,b,c; Hissa, 1968; Hill, 1976; Tacu, 1978; Poczipko, 1979). Additional studies have used a combination of the previous two methods (cooling curves and oxygen consumption) and have recorded body temperature and oxygen consumption simultaneously (Hahn, 1956a,b,c; Hahn et al., 1956; Dawkins and Hull,

1964; Hull, 1965; Bruck and Wunnenberg, 1966; Gebczynski, 1970; Noll, 1979; Takano et al., 1979; Dolman, 1980).

One drawback of the combination method is that one cannot be certain of what effect attachment of the thermocouple(s) to the animal has on the oxygen consumption of the animal. If attachment of a thermocouple to an animal causes increased activity (agitation, struggle, etc.), the determination of oxygen consumption will yield a higher estimate than one determined for the animal without thermocouples attached. Therefore, in the present study, body temperatures of neonates were measured prior to and immediately after measurements of oxygen consumption. These measurements still permit the calculation of an average rate of fall in body temperature or the plotting of the final body temperature (Hill, 1976).

The degree of thermoregulatory ability in neonates is dependent upon such factors as body size, thermal insulation, degree of neurological control and thermogenic capability at birth (Hull, 1973). Large neonates, such as newborn lambs, have thermoregulatory abilities quite similar to adults (Alexander, 1961, 1962a,b; Alexander and Williams, 1962), and are able to maintain homeothermy when subjected to ambient temperatures as low as -10 C. Newborn caribou, due to their large size and well-developed thermal insulation, thermoregulate with no apparent difficulty and are in thermal danger in the arctic only under wet, windy conditions (Lentz and Hart, 1960; Hart et al., 1961). On the other hand, neonates such as the human (Hill and Rahimtulla, 1965; Hey and Katz, 1970; Hey et al., 1970) and the pig (Mount, 1959, 1964)

are born with little thermal insulation (also, in the human, poor motor development); consequently, both species are relatively poor thermoregulators as neonates.

The smaller the neonate (as with any adult), the greater the thermoregulatory problems associated with the mass/surface area relationship (Brody, 1945; Kleiber, 1947; Hull, 1973; Farkas, 1979). However, dependent upon the degree of development of thermal insulation, motor control, energy stores (e.g., brown adipose tissue) and the rapidity of postnatal growth, small neonates such as the rabbit (Dawes and Mestyan, 1963; Dawkins and Hull, 1964; Hull, 1965; Hull and Segall, 1965a,b,c), guinea pig (Dawes and Mestyan, 1963; Bruck and Wunnenberg, 1965, 1966), kitten (Hull, 1965; Olmstead et al., 1979), puppy (Hull, 1973) and bushbaby (Dobler, 1976) can maintain homeothermy over a wide range of temperatures (above 15 C) in a relatively short period of time. Very small neonates, such as mice (Fitzgerald, 1953; Lagerspetz, 1962; Cassin, 1963; Chew and Spencer, 1967; Gebczynski, 1970; Hudson, 1974; Bryant and Halls, 1975; Stainer, 1975; Hill, 1976; Sales and Skinner, 1979), gerbils (McManus, 1971), hamsters (Hissa, 1964, 1968), ground squirrels (Maxwell and Morton, 1975; Tacu, 1978; Dolman, 1980), lemmings and voles (Morrison et al., 1954; Hissa, 1964, 1968), bats (Weigold, 1973; Noll, 1979) and rats (Hahn, 1956a,b,c; Hahn et al., 1956; Taylor, 1960; Blackmore, 1970; Takano et al., 1979), are extremely dependent upon huddling and maternal care for survival, especially immediately after birth. In these animals, attainment of homeothermy is a gradual process with considerable variability among

species (lemming: 11 days (Hissa, 1964), ground squirrel: 45 days (Maxwell and Morton, 1975); with 18 days the most common age of attainment of homeothermy).

In a category by themselves are neonates of the more primitive mammalian orders (monotremes, marsupials). Because of the unique reproductive strategy of marsupials, their neonates have a rather lengthy developmental period before adult thermoregulatory characteristics are attained (Morrison and Petajan, 1962). There is no information available on thermoregulatory abilities of neonatal monotremes.

Also unique in thermoregulatory ability at birth are many of the large polar dwelling mammals (Blix and Steen, 1979). The ability of these animals to thermoregulate soon or immediately after birth (especially members of the pinniped and whale families), is thought to be related to the large amount of fat and/or fur insulation, heat exchangers and extremely calorie-rich milk from the mother (Blix and Steen, 1979).

Nonshivering thermogenesis (NST) and shivering thermogenesis (ST) are two endothermic processes that are essential for attainment of homeothermy in most neonates (Hull, 1973). Generally, the primary sites for NST have been shown to be located in brown adipose tissue (BAT) deposits in the interscapular region (Dawkins and Hull, 1964), skeletal muscles (Jansky, 1973) and around various organs and major blood vessels of the neck (Hull, 1973). Considerable interspecies variation exists in the relative amounts of BAT present at the different sites (Dawkins and Hull, 1964). Bruck et al. (1969) and

Jenkinson et al. (1968) have reported the total absence of NST during postnatal development in the pigmy pig and ox calf, respectively. Shivering thermogenesis naturally, is restricted to the muscle masses of the body.

Nonshivering thermogenesis has been shown to be extremely important to the neonate in the first days of life (Bruck and Wunnenberg, 1966). Hull and Segall (1965a) removed various amounts of BAT from newborn rabbits and noted a proportional reduction in total oxygen consumption. The importance of NST is succeeded by ST (except in the pigmy pig and ox calf which exhibit no NST) as the neonate matures (Bruck and Wunnenberg, 1965, 1966; Hissa, 1968; Arjamaa and Lagerspetz, 1979).

The age at which NST is replaced by ST is dependent upon the degree of anatomical development at birth (Jansky, 1973) and has been closely correlated with postnatal maturation of the nervous system (Buchanan and Hill, 1949; Hahn, 1956a,c; Hahn et al., 1956; Lagerspetz, 1962; Hissa, 1968; Lapointe and Nosal, 1979). In addition, Maxwell and Morton's (1975) study on development of thermoregulation in the Belding ground squirrel (a hibernator) and the antelope ground squirrel (a nonhibernator), found that onset of visible shivering occurred by day 15 in the hibernator and day 25 in the nonhibernator. Furthermore, adult-like thermoregulatory ability was achieved at an earlier age by the hibernator (25 days) than the nonhibernator (45 days). Maxwell and Morton (1975) hypothesized that early attainment of thermoregulatory ability in the hibernator was adaptive in that it enabled early emergence from the burrow. Early emergence would permit sufficient

time for attainment of appropriate body size and fat reserves necessary for survival of the oncoming hibernation period. In more precocial neonates (e.g., lambs, kittens), NST reaches its greatest endothermic potential shortly after birth (Jansky, 1973). On the other hand, in small rodent species that are born in a more altricial state, NST develops and approaches peak endothermic potential 1 to 2 weeks after birth (Jansky, 1973). Subsequently, the endothermic role of NST in the neonate is replaced by ST (Bruck and Wunnenberg, 1966; Hissa, 1968; Jansky, 1973). Jansky (1973) has written an extensive review of the literature on NST and its thermoregulatory significance both in the neonate and in the adult. Additional information on recent studies on the control of NST can be found in Girardier and Seydoux (1978).

The young of Sigmodon hispidus are born in an advanced stage of development when compared to other small species of rodents (Randolph et al., 1977). Young cotton rats at birth are partially furred and generally weigh between 5-8 grams (Golley, 1962; Kilgore, 1970). The average litter size ranges between 3.4 to 9.0 and is dependent upon such factors as latitude, season of the year and age and size of the mother (Kilgore, 1970; Fleharty and Choate, 1973; McCleughan and Gaines, 1978). Although larger litters are produced by cotton rats in the more northern latitudes, size of the individual at birth is not significantly different from that of young born in the more southern latitudes (Kilgore, 1970). Neonatal cotton rats open their eyes at approximately 18 to 36 hours of age (Meyer and Meyer, 1944) and are weaned between 15-25 days of age (Meyer and Meyer, 1944; Golley, 1962). Odum (1955)



reported captures away from the nest, of individuals estimated to be as young as 4 days of age.

### Thermoregulation in Adults

Few studies have examined metabolic rates in the hispid cotton rat. However, before these studies can be properly compared, several definitions need to be made (according to Bartholomew, 1977):

- 1) Basal Metabolic Rate (Standard Metabolic Rate) = the metabolic rate of a postabsorptive, resting animal in thermoneutrality
- 2) Resting Metabolic Rate = basal metabolic rate + cost of thermoregulation at ambient temperatures outside the thermal neutral zone
- 3) Average Daily Metabolic Rate = resting metabolic rate + cost of activity + specific dynamic action + production over a 24 hour period

The degree of elevation in metabolic rate due to specific dynamic action (SDA) may vary from 3-50 % of fasting metabolic rate (Brody, 1945). The amount of variation is dependent not only upon the levels of carbohydrate, fat and protein of the food consumed, but also on the "plane of nutrition" of the animal (i.e., what degree of starvation the animal is in prior to consumption of food), and the ambient temperature at which the animal is tested (Brody, 1945; Kleiber, 1961). Therefore, values reported in the literature for animals not in a post-absorptive state may exhibit greater variation (and thereby increase the difficulty of comparison) than equivalent values determined for

animals in a postabsorptive state. Since individual differences within a species may exist in the rate of attainment of postabsorptiveness, animals not in a postabsorptive state may exhibit additional variation in metabolic rates (above that of intrinsic differences) due to the SDA contribution. Such variations may obscure differences in the metabolic responses exhibited by S. h. texianus from Kansas and Texas when exposed to a given ambient temperature. Thus, all adult animals tested in the present study were in the postabsorptive state.

Gaertner (1968) has produced the most comprehensive work on metabolism in the hispid cotton rat. Gaertner (1968) determined daily energy budgets, patterns of activity, rates of metabolism and thermoregulatory abilities in adult hispid cotton rats from Arkansas during each season of the year. Animals were collected each season and were held in the laboratory in environmental chambers which simulated the appropriate photo and thermal cycles for the appropriate season. Therefore, animals tested in Gaertner's (1968) study expressed the appropriate state of acclimatization for spring, summer, fall or winter. Of primary interest to the present study are the data on thermoregulatory abilities of Sigmodon hispidus during each season. Gaertner (1968) determined basal metabolic rates of S. hispidus to be 0.99, 0.94, 1.00 and 1.26 ml O<sub>2</sub>/g.h in the spring, summer, fall and winter, respectively. The lower critical temperature of the thermoneutral zone was determined to be approximately 28 C in spring, 30 C in summer, 28 C in fall and 29 C in winter. Gaertner (1968) did not report upper critical temperatures for the thermoneutral zones in

spring, summer and fall; however, for winter, the upper critical temperature was reported to be approximately 33.3 C (i.e., thermoneutral zone = 29-33.3 C in winter).

Wagner (1970) examined metabolic rates of free-living S. hispidus in South Carolina by correlation of excretion rates of  $^{32}\text{P}$  with rates of oxygen consumption. A significant correlation was found between rates of excretion of  $^{32}\text{P}$  and rates of oxygen consumption in acclimatized animals tested at known ambient temperatures in the laboratory. Based on that correlation, Wagner (1970) predicted average rates of oxygen consumption (average daily metabolic rates) in free-living S. hispidus to be 2.37, 3.41 and 4.02 ml  $\text{O}_2/\text{g}\cdot\text{h}$  in July, September and November, respectively.

Bowers (1971) determined resting metabolic rates in five species of Sigmodon. Of the five species in Bowers' (1971) study, one was Sigmodon hispidus, for which five subspecies from different regions of North and Central America were examined: S. h. texianus (from Arkansas), S. h. berlandieri (from Texas), S. h. toltecus (from Veracruz), S. h. chiriquensis (from Panama) and S. h. mascotensis (from Jalisco). Of these five subspecies only one, S. h. toltecus, has a resting metabolic rate that is significantly different from those of the other members of the S. hispidus ssp. group (2.42 ml  $\text{O}_2/\text{g}\cdot\text{h}$  for S. h. toltecus and an average of 1.46 ml  $\text{O}_2/\text{g}\cdot\text{h}$  for the other four subspecies). Resting metabolic rates in the S. hispidus ssp. group show a general pattern; higher resting metabolic rates in animals inhabiting areas with ample access to food and water (e.g., 2.42 ml  $\text{O}_2/\text{g}\cdot\text{h}$  for S. h. toltecus) and

lower resting metabolic rates in animals inhabiting more xeric areas (e.g., 1.31 ml  $O_2$ /g·h for S. h. texianus). This pattern is consistent with that previously reported for other species (Dawson, 1955; Bartholomew and MacMillan, 1961; McNab and Morrison, 1963; Carpenter, 1966; Hudson et al., 1972; McNab, 1979).

Randolph et al. (1977) examined rates of oxygen consumption in nonreproductive, pregnant and lactating female hispid cotton rats maintained in the laboratory. It was found that animals in these three reproductive conditions have similar resting metabolic rates when exposed to an ambient temperature of 20 C.

In Wagner's (1970), Bowers' (1971) and Randolph's et al. (1977) studies on metabolic rates in S. hispidus, values reported for oxygen consumption include that portion contributed by specific dynamic action (SDA) and therefore, do not reflect the true basal metabolic rates (postabsorptive animal in thermoneutrality) or resting metabolic rates (postabsorptive animal above or below thermoneutrality). Gaertner (1968) withheld food 2 hours prior to tests for determination of metabolic rates; but the values reported for oxygen consumption probably represent levels of metabolism that are partially attributable to the effects of SDA. Brown (1968) reported that Neotoma required up to 7 hours of food deprivation before a postabsorptive state (no SDA effect) was achieved. Hudson and Deavers (1973) reported a minimum period of 24 hours of food deprivation to ensure that Spermophilus became postabsorptive prior to metabolic testing. Consequently, the values reported by Gaertner (1968) for oxygen

consumption in S. hispidus most likely do represent levels of metabolism that are partially due to SDA.

#### Explanation of Dissertation Format

This dissertation is written in the alternate format style. The first section entitled, "A comparison of thermoregulation and evaporative water loss in the hispid cotton rat, Sigmodon hispidus texianus, from northern Kansas and south-central Texas," is written in the format required by the scientific journal, Ecology, to which it will be submitted for publication. The second section entitled, "Development of thermoregulation in the neonatal hispid cotton rat, Sigmodon hispidus texianus, from northern Kansas and south-central Texas," is written in the format required by the scientific journal, Physiological Zoology, to which it will be submitted for publication. New information reported in the two papers contained within this dissertation is solely the result of endeavors carried out by the candidate.

A COMPARISON OF THERMOREGULATION AND EVAPORATIVE  
WATER LOSS IN THE HISPID COTTON RAT,  
SIGMODON HISPIDUS TEXIANUS,  
FROM NORTHERN KANSAS AND SOUTH-CENTRAL TEXAS

## INTRODUCTION

The hispid cotton rat, Sigmodon hispidus texianus, is an herbivorous species which generally inhabits mesic areas (Martin, 1960; Fleharty and Mares, 1973). The range of S. h. texianus extends from south-central Texas northward to extreme northern Kansas and from western Missouri, Arkansas and Louisiana westward to eastern Colorado and the Oklahoma and Texas panhandles (Hall and Kelson, 1959). The recent northward dispersal of S. h. texianus into increasingly temperate regions has received considerable documentation (see Cockrum, 1948 and Genoways and Schlitter, 1966 for reviews).

The genus Sigmodon is subtropical in origin and for the most part, distribution (Hibbard, 1960); consequently, animals at the northern periphery are at times subjected to environments which may be extremely inhospitable to them. However, S. h. texianus has continued to extend its range northward. Indeed, captures of this species have been reported for extreme south-central (Genoways and Schlitter, 1966) and south-eastern (Liesveld and Fiala, 1977) Nebraska. It is unlikely that this movement northward through Kansas (within the last century) can be linked to general climatic changes on the Great Plains since the climatic regime in this region of North America has not changed as abruptly as the northern movement of S. h. texianus (Hoffmann and Jones, 1970).

Several studies (Kilgore, 1970; Bowdre, 1971; McCleughan and Gaines, 1978; Cameron et al., 1979b) have examined various aspects of the biology of S. h. texianus at different latitudes. These studies

have noted changes in the behavior and physiology of the species in order to cope with the climatic regimes of the more northern latitudes (37-40° N lat.). It has been hypothesized that the stress imposed upon S. h. texianus by exposure to severe cold weather is probably the primary factor in determination of the northern boundary for the distribution of this subspecies (Fleharty et al., 1972). Under such conditions, individuals that are genetically more "cold-hardy" than others would be more able to cope with and survive the harsher winters of the more northern latitudes.

One widely accepted index of cold-hardiness is the ability of an animal to adequately thermoregulate when exposed to low ambient temperatures. An animal that is genetically adapted (in addition to common acclimitization changes for winter) for an increased ability to regulate its body temperature can withstand cold exposure (at least for short periods of time) more successfully than one who is not equally adapted. Such an advantage may play a significant role in winter survival, especially when considering the alternatives of undergoing "cold weather starvation" (remaining in the nest during periods of extreme cold) (Howard, 1951) or foraging for food during extremely cold temperatures. This potential advantage (adaptive ability for increased resistance to cold exposure), would necessitate that such forages for food produce a net energy gain, i.e., the animal collects more energy via food consumed and assimilated than is expended during the foraging episode.



The object of this paper is to present and compare data on thermoregulatory abilities for possible phylogenetic differences of laboratory-reared S. h. texianus from northern Kansas and south-central Texas, regions that are near the northern and southern limits of the range of this subspecies.

## METHODS AND MATERIALS

## Source and Maintenance of Animals

Adult specimens of Sigmodon hispidus texianus were obtained from localities near College Station, Texas and Hays, Kansas. Within 2 weeks of capture, animals were shipped by air to Iowa State University where this study was undertaken.

Animals were maintained on a 14L:10D photoperiod at  $23 \pm 2$  C which is within the range of optimal conditions for the breeding of cotton rats in captivity (Meyer and Meyer, 1944; Johnston and Zucker, 1979). Adult animals were provided with Teklad 4 % Mouse and Rat Chow only during the dark phase of the photoperiod cycle. Restricted access to food ensured that animals did not become obese. Food was available ad libitum to juveniles and lactating females. Water was available ad libitum to all animals. Males and females were paired and housed in 45 x 25 x 20 cm cages. Three cm of wood shavings were placed in all cages for bedding. Males were removed from the cage shortly before or within 12 hours after birth of young.

Sixteen wild-caught animals from Texas and ten wild-caught animals from Kansas were used for production of offspring used in experimentation. Weaned litters were separated by sex and siblings of each sex were housed together in 45 x 25 x 20 cm cages until 5 months old. By the 5th month, animals had achieved body weights similar to those reported in the literature for wild-caught adults (Meyer and Meyer, 1944; Fleharty and Choate, 1973; McClellaghan and Gaines, 1978).

Five male and 5 female offspring were randomly chosen from each group (Texas, Kansas) of 5 month-old rats for experimentation. These animals were housed separately in 25 x 12 x 18 cm cages at least 6 weeks prior to and throughout the duration of experimentation.

Various authors have reported activity patterns of S. hispidus to be arrhythmic (Selander and Walker, 1959), diurnal (Bailey, 1902; Aldrich and Bole, 1937) or crepuscular (Harper, 1927; Cameron et al., 1979a; Kilduff and Dube, 1979). Calhoun (1945) concluded that S. hispidus possessed "very labile nocturnal patterns" which could be modified by biotic and environmental factors. Bowers (1971) reported that 5 species of cotton rats maintained in the laboratory were least active during daylight hours. Animals in the present study were observed to reflect a similar pattern of activity. Therefore, examination of thermoregulatory parameters of the animals in this study was conducted within the light phase of the daily photoperiod cycle.

#### Respirometry

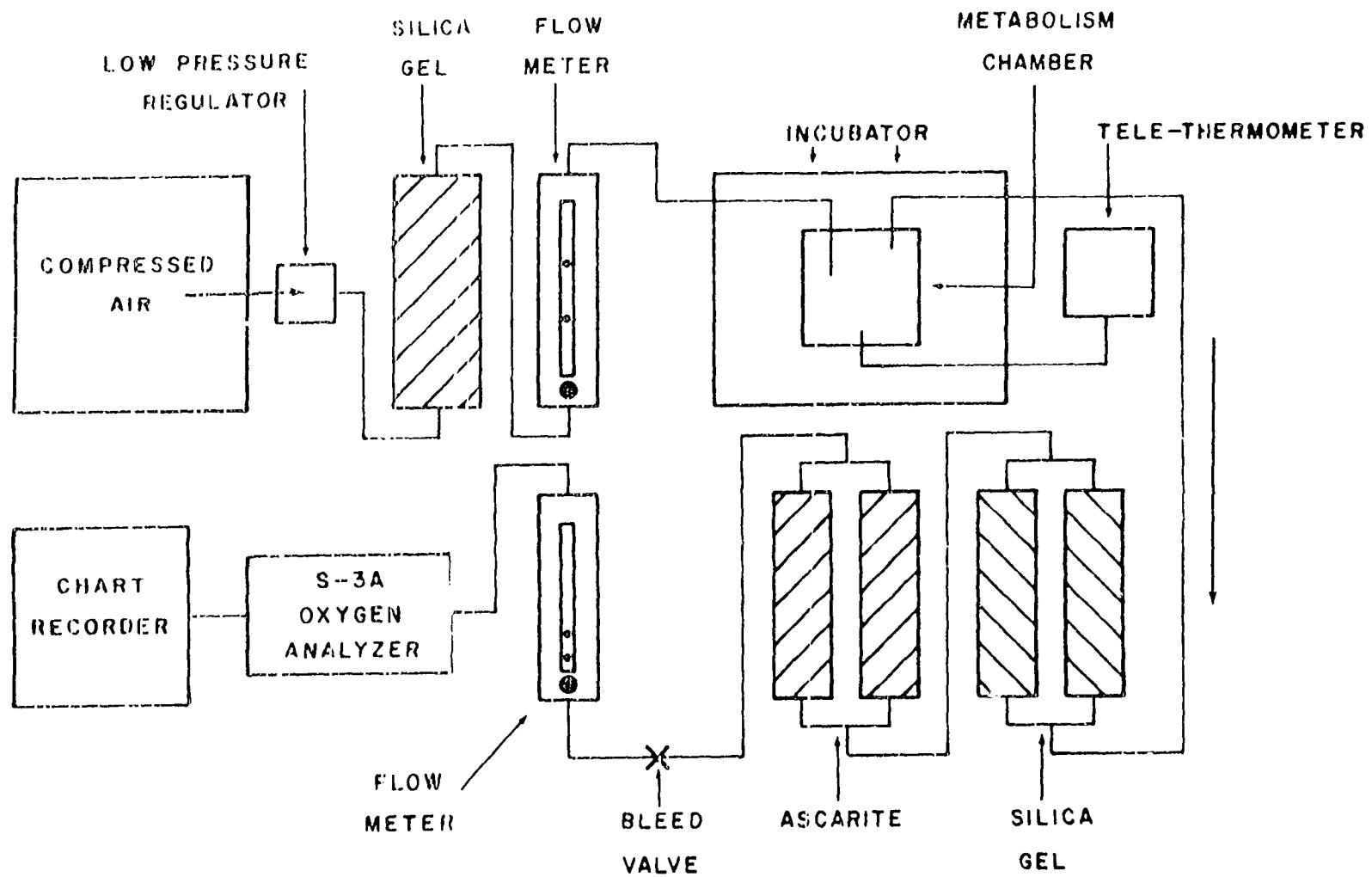
Oxygen consumption was determined by open system respirometry (Depocas and Hart, 1957). The metabolism chamber consisted of an 18 liter square can with a wire mesh platform placed 5 cm above the bottom of the can for the animal to rest upon. Beneath the platform, a layer of paraffin oil was added to prevent evaporation of moisture from urine or feces voided by the animal while in the chamber. Openings in the lid of the can permitted placement of incurrent and excurrent ducts for air and a YSi temperature probe for measurement of chamber temperature. Compressed air was passed through a column of

silica gel (to remove moisture), regulated to a flow of 1800 ml/min with a Brooks 1110 factory calibrated flowmeter and passed through the metabolism chamber. Excurrent air was passed through columns of silica gel and Ascarite (to remove  $\text{CO}_2$ ). A portion of the dry, carbon dioxide-free excurrent air was diverted to an oxygen analyzer (Applied Electrochemistry S-3A) for analysis of oxygen content. Output from the oxygen analyzer was recorded by a Houston Instruments strip chart recorder. A schematic diagram of the respirometry system can be seen in figure 3.

Animals were tested, individually, at ambient temperatures between 0 and 40 C. After introduction of an animal into the metabolism chamber, the chamber was sealed and placed in a Precision Instruments Model 815 low-temperature incubator. The internal temperature of the chamber was maintained to within 0.1 C of the desired temperature. Initial and final body temperatures were taken by insertion of a Schuitheis thermometer 2 cm into the rectum. Initial and final body weights were measured to the nearest 0.1 gram.

Bowers (1971) found that if individuals of Sigmodon spp. are denied food (for 12 hrs) prior to metabolic determinations, they become "highly active" in the metabolism chamber. However, animals in the present study exhibited no increase in activity in the metabolism chamber when food was withheld. Therefore, all animals in the present study were tested while in the postabsorptive state. Animals in the present study were determined to require a minimum of 8 hours of food deprivation before a totally postabsorptive state was achieved.

Fig. 3. Schematic diagram of the apparatus used for determination of  $O_2$  consumption, evaporative water loss and  $CO_2$  production.



When oxygen consumption became minimal and repeatable, water (from pulmocutaneous evaporation) and carbon dioxide (produced by the animal) were collected with pre-weighed columns of silica gel and Ascarite, respectively. After a minimum of 15 minutes of water and carbon dioxide collection, the columns were reweighed to the nearest 0.1 mg on a Mettler H33 balance and changes in weights were recorded. If the animal became active during the collection period, the values obtained were discarded. After a metabolic measurement was completed at a given ambient temperature ( $T_a$ ), the animal was removed from the metabolism chamber and final body temperature and final body weight determined. An average of the initial and final body weights was used for subsequent calculations of values obtained at that  $T_a$ . Animals were tested at no more than 3  $T_a$ 's on a given day with most animals tested at only 1 or 2  $T_a$ 's on the same day. Animals were subjected to each  $T_a$  for a minimum of 3-4 hours.

If the animal was tested at a 2nd or 3rd  $T_a$ , the same procedures were repeated; including measurement of body temperature and body weight. The new  $T_a$  was at least 10 C higher than the previous one. Approximately 30 minutes were required for stabilization of the new temperature of the chamber prior to initiation of the 2nd or 3rd tests. Animals were kept in the chamber throughout this period. The initial  $T_a$  to which an animal was subjected on a given day was selected at random. A period of at least 7 days transpired between consecutive test days of any individual animal. Weight loss suffered during the starvation period and subsequent experimentation was regained between test days.

## RESULTS

Data obtained for male or female cotton rats from a given lineage (Kansas, Texas) did not differ; therefore, data obtained from both sexes were pooled. (Hereafter, cotton rats of Kansas and Texas lineages shall simply be referred to as Kansas animals and Texas animals.) All data were obtained during the months of January-June in both 1979 and 1980. Average body weights (in grams) were  $152.4 \pm 5.1$  (2SE), range = 113.6-209.4 and  $140.5 \pm 3.6$  (2SE), range = 107.3-169.8 for Kansas animals and Texas animals, respectively. In future discussion, all values presented represent  $\bar{x} \pm 2$  SE.

## Oxygen Consumption

The relationship of oxygen consumption to ambient temperature ( $T_a$ ) can be seen in figures 4a and 4b for Sigmodon hispidus texianus from Kansas and Texas, respectively.

Kansas animals

The thermoneutral zone covered approximately 5 C extending from 29.0 to 33.7 C (Fig. 4a). Basal metabolism in ml  $O_2$ /g·h was determined to be  $0.83 \pm 0.06$  which is 85 % of the value predicted from body weight using the allometric equation of Morrison et al. (1959):  $M = 3.8 W^{-0.27}$ . The line depicting  $O_2$  consumption vs  $T_a$  below 29 C extrapolates to zero metabolism at 41.6 C (Eq. 1, Table 1). Above thermoneutrality  $O_2$  consumption increases at a greater rate than that below thermoneutrality (Eq. 2, Table 1). When rates of  $O_2$  consumption are corrected to a standard body weight  $w_b^{0.73}$  (Brody, 1945) and data expressed in this



Fig. 4a. Relationship between O<sub>2</sub> consumption in Sigmodon hispidus texianus of Kansas lineage and ambient temperature. Zone of thermoneutrality is from 29.5 to 33.7 C.

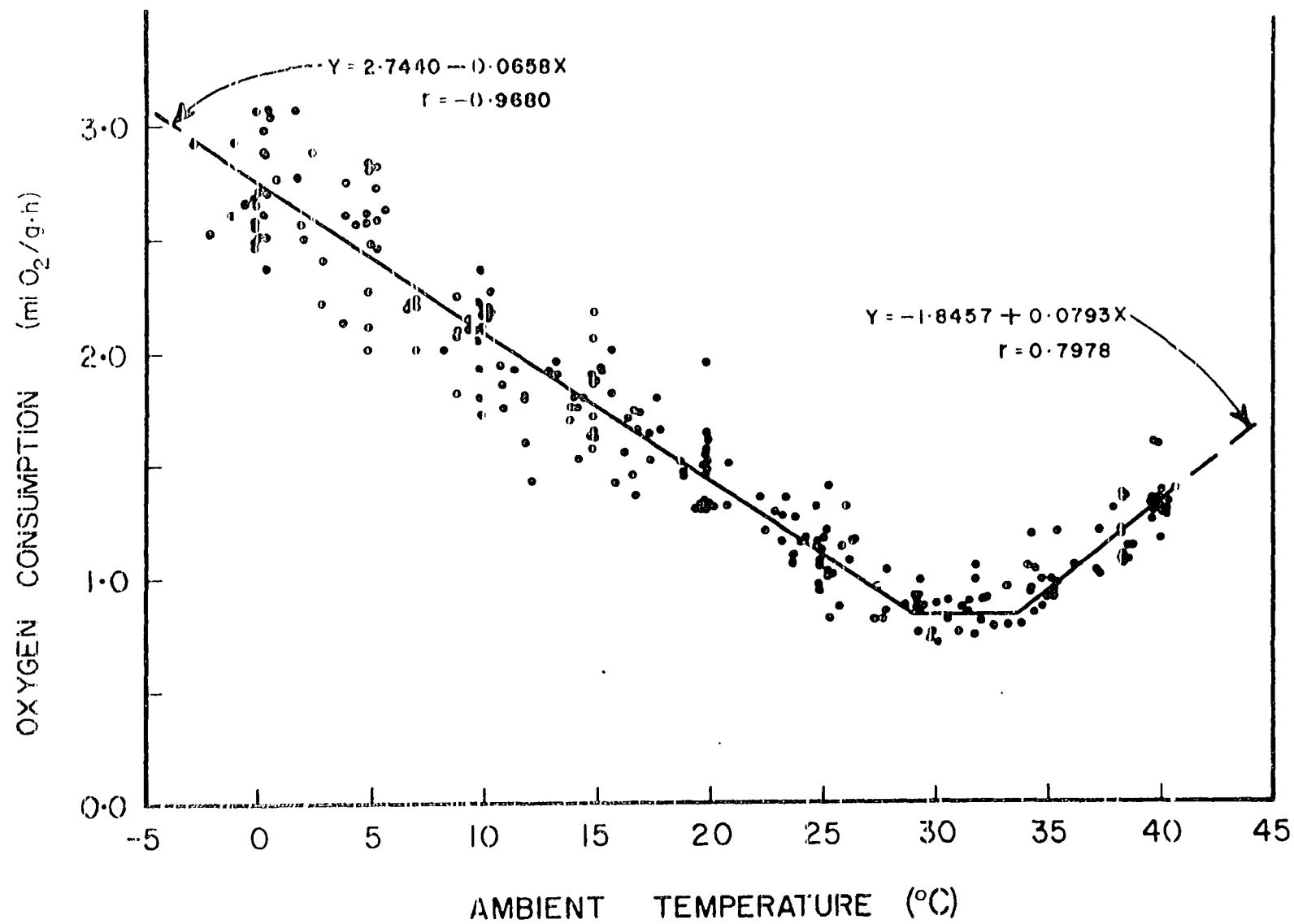


Fig. 4b. Relationship between  $O_2$  consumption in Sigmodon hispidus texianus of Texas lineage and ambient temperature. Zone of thermoneutrality is from 33.5 to 35 C.

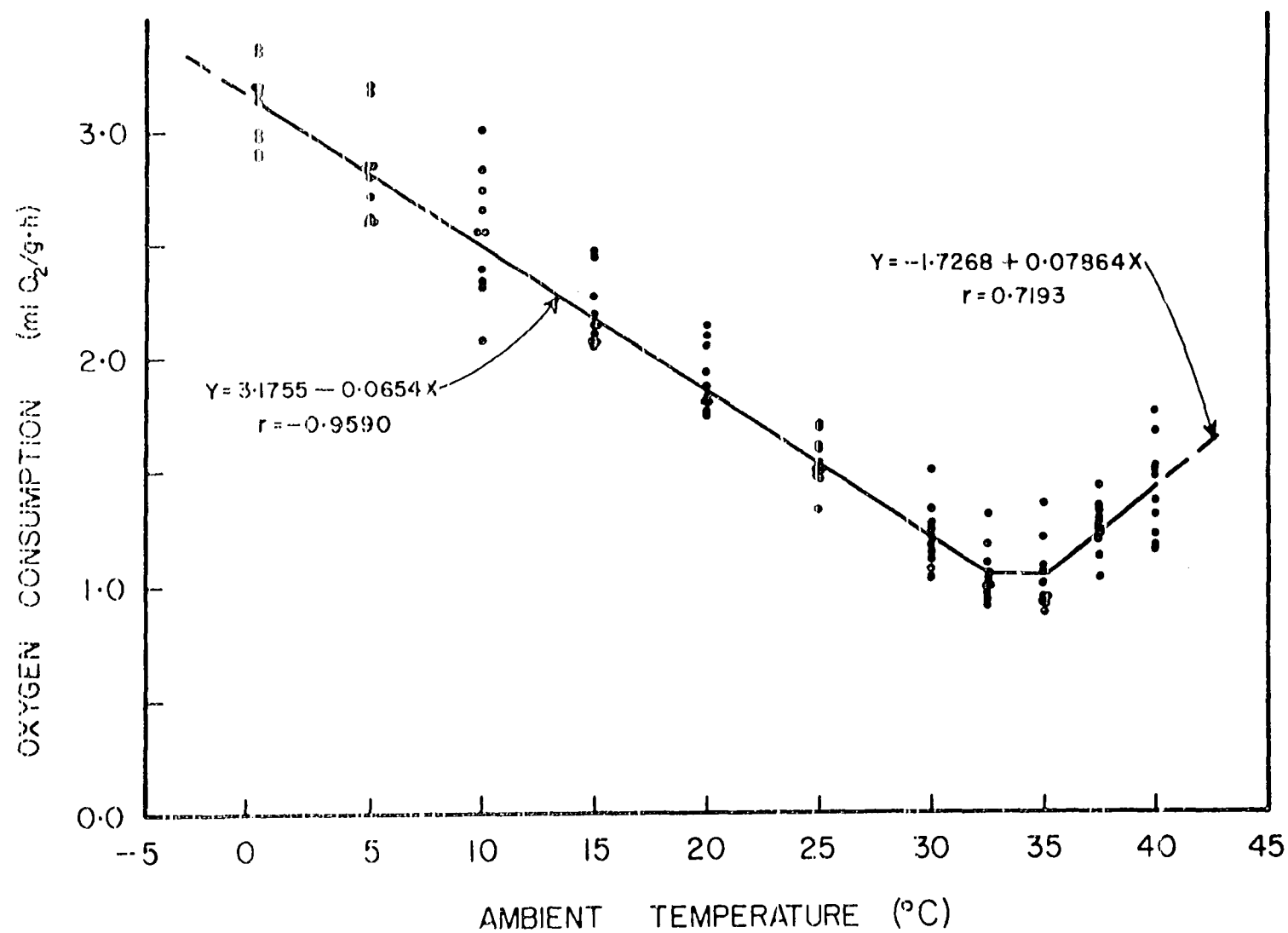


Table 1. Relationship of physiological variables to ambient temperature ( $T_a$ ) in Sigmodon hispidus texianus of Kansas and Texas lineages

Eq.	Lineage	$T_a$ Range	Linear Regression Equation	Correlation Coefficient (r)
$O_2$ consumption ml $O_2$ /g·h				
1	Kansas	0-29.5	= $2.74 - 0.0658T_a$	- 0.968
2	Kansas	33.7-40	= $-1.85 + 0.0793T_a$	0.798
3	Texas	0-32.5	= $3.18 - 0.0654T_a$	- 0.959
4	Texas	35-40	= $-1.73 + 0.0786T_a$	0.719
Evaporative water loss mg $H_2O$ /ml $O_2$				
5	Kansas	0-20	= $0.464 + 0.0355T_a$	0.695
6	Texas	0-20	= $0.714 + 0.0166T_a$	0.435
Total conductance ml $O_2$ /g·h·°C				
7	Kansas	0-25	= $0.076 + 0.0001T_a$	0.150
8	Texas	0-20	= $0.081 + 0.0012T_a$	0.645
% Metabolic heat evaporated				
9	Kansas	0-20	= $5.83 + 0.5040T_a$	0.668
10	Kansas	35-39	= $-82.9 + 2.6232T_a$	0.859
11	Texas	0-20	= $1.90 + 0.2210T_a$	0.749
12	Texas	35-40	= $-51.7 + 1.6936T_a$	0.817
Dry conductance ml $O_2$ /g·h·°C				
13	Kansas	0-20	= $0.072 - 0.0003T_a$	- 0.339
14	Texas	0-20	= $0.078 + 0.0010T_a$	0.671
Body temperature (°C)				
15	Kansas	0-31.5	= $38.2 - 0.0084T_a$	- 0.252
16	Kansas	31.5-40	= $26.9 + 0.3554T_a$	0.854
17	Texas	0-32.5	= $38.1 - 0.0001T_a$	- 0.005
18	Texas	32.5-40	= $26.6 + 0.3552T_a$	0.919

fashion, results obtained do not significantly differ from those based upon data expressed on a per gram basis. Therefore, all data reported are expressed on a per gram basis.

#### Texas animals

The thermoneutral zone covered a range of approximately 2.5 C extending from 32.5 to 35.0 C (Fig. 4b). Basal metabolism in ml  $O_2$ /g·h was found to be  $1.03 \pm 0.06$  which is 103 % of the value predicted from weight. Below thermoneutrality, the line representing  $O_2$  consumption vs  $T_a$  extrapolates to zero metabolism at 48.6 C (Eq. 3, Table 1). Above thermoneutrality,  $O_2$  consumption increases at a greater rate than  $O_2$  consumption below thermoneutrality (Eq. 4, Table 1). As in the case of Kansas animals, when  $O_2$  consumption of Texas animals is corrected to a standard body weight results obtained are not significantly different from those expressed simply on a per gram basis. Thus, all data reported for Texas animals also are reported on a per gram basis.

#### Body Temperature

#### Kansas animals

Rectal  $T_b$ 's range between 37.0-39.0 C ( $38.1 \pm 0.1$ ) in quiescent animals exposed to  $T_a$ 's between 0-33.5 C (Eq. 15, Table 1; Fig. 5a). Body temperature increases with  $T_a$  at  $T_a$ 's above 35.5 C (Eq. 16, Table 1). The highest  $T_b$  (41.4 C) was recorded from an animal exposed for three hours to a  $T_a$  of 41.1 C.

Fig. 5a. Relationship between body temperature in Sigmodon hispidus texianus of Kansas lineage and ambient temperature.

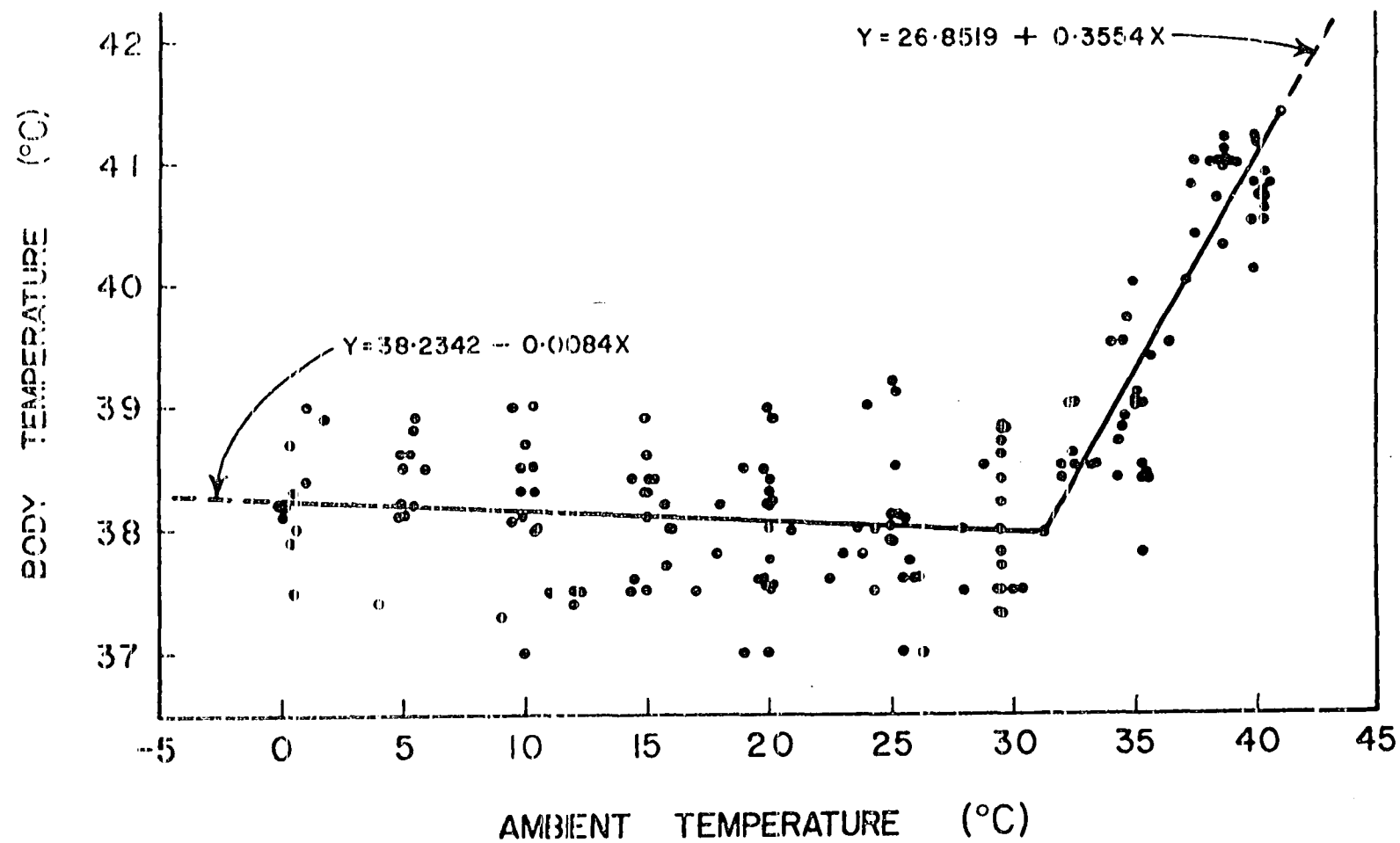
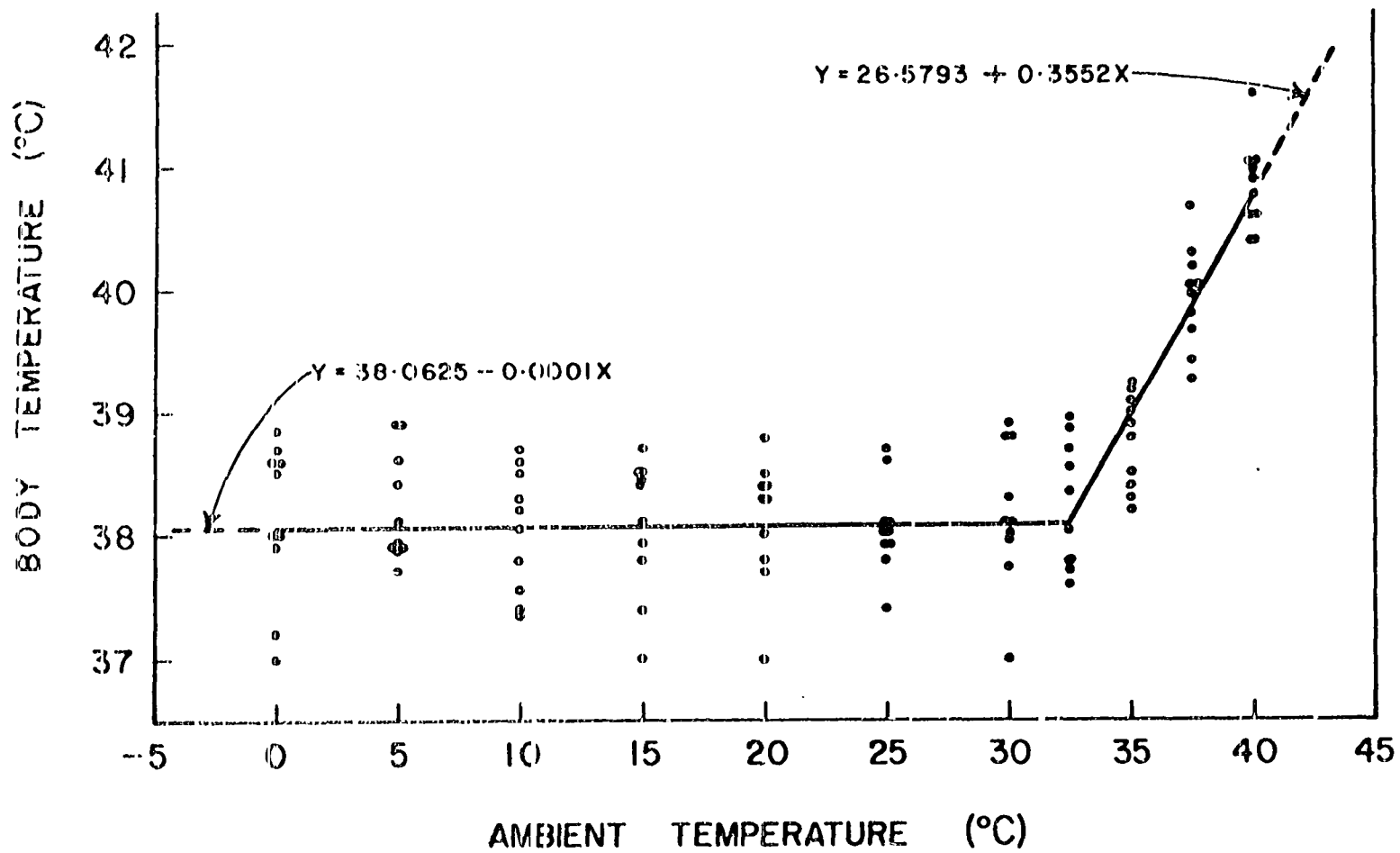




Fig. 5b. Relationship between body temperature in Sigmodon hispidus texianus of Texas lineage and ambient temperature.



Texas animals

Rectal  $T_b$ 's range between 37.0-39.0 C ( $38.1 \pm 0.1$ ) in quiescent animals exposed to  $T_a$ 's between 0-32.5 C (Eq. 17, Table 1; Fig. 5b). Body temperature increases with  $T_a$  at  $T_a$ 's above 35 C (Eq. 18, Table 1). The highest  $T_b$  (41.6 C) was recorded for an individual exposed for 3.5 hours to a  $T_a$  of 40.0 C.

## Evaporative Water Loss

Kansas animals

Evaporative water loss in mg  $H_2O$ /ml  $O_2$  is lowest ( $0.51 \pm 0.1$ ) at  $T_a = 0$  C and highest ( $9.74 \pm 0.6$ ) at  $T_a = 40$  C (Fig. 6a). Little variation occurs in rates of evaporative water loss (EWL) at  $T_a$ 's of 0-20 C (Eq. 5, Table 1). Above 20 C evaporative water loss increases curvilinearly (Fig. 6a). The range of values recorded at  $T_a$ 's above 20 C is considerably larger than values recorded at  $T_a$ 's below 20 C. Values indicated in figure 6a for EWL at  $T_a = 40$  C are probably conservative estimates because moisture condensation at this  $T_a$  occurred in the lines carrying the excurrent flow of air. Animals when exposed to a  $T_a$  of 40 C salivated very profusely wetting the entire ventral surface of the body and the entire facial area. The animals were also seen to be profusely drooling from the mouth (which was held open) when removed from the metabolism chamber (after a 3-4 hour exposure at  $T_a = 40$  C). Because accurate measurements of EWL were not obtained at  $T_a = 40$  C, all future discussion referring to responses of Kansas animals at "highest  $T_a$ " (except that for total conductance), shall pertain to

Fig. 6a. Relationship between evaporative water loss  
in Signodon hispidus texianus of Kansas lineage  
and ambient temperature.

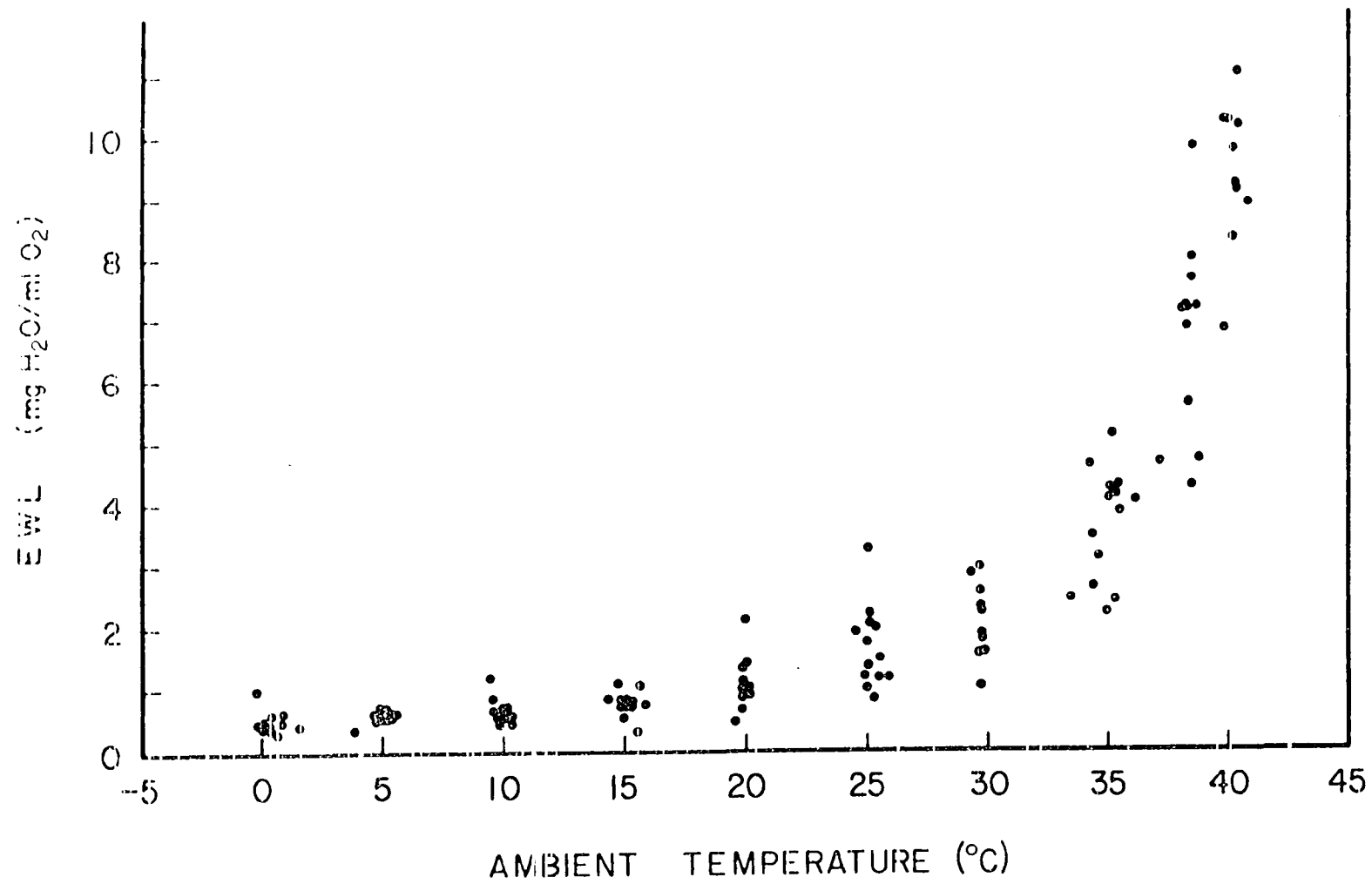


Fig. 6b. Relationship between evaporative water loss  
in Sigmodon hispidus texianus of Texas lineage  
and ambient temperature.



data collected at  $T_a = 39$  C. Values of absolute water loss (in mg  $H_2O/g \cdot h$ ) at various  $T_a$ 's can be found in Table 2.

Table 2. Water loss in mg  $H_2O/g \cdot h \pm 2$  SE by S. h. texianus at various  $T_a$ 's

$T_a$	Kansas	Texas
0	$1.5730 \pm 0.1983$	$1.9742 \pm 0.2824$
5	$1.7375 \pm 0.1548$	$1.7919 \pm 0.7401$
10	$1.7017 \pm 0.2000$	$1.9789 \pm 0.2235$
15	$1.9550 \pm 0.2116$	$2.2603 \pm 0.5729$
20	$1.9800 \pm 0.3449$	$2.3897 \pm 0.3844$
25	$2.1508 \pm 0.4950$	$2.3058 \pm 0.2319$
30	$2.3863 \pm 0.6609$	$2.3455 \pm 0.5265$
35	$3.6433 \pm 0.4740$	$2.9914 \pm 0.6215$
40	$12.9873 \pm 1.2270^a$	$12.6069 \pm 1.0517$
	$7.4470 \pm 0.8998^b$	

<sup>a</sup>Conservative value due to moisture condensation in excurrent line (see text).

<sup>b</sup>Value for  $T_a = 39$  C.

#### Texas animals

Evaporative water loss in mg  $H_2O/ml$   $O_2$  is lowest ( $0.68 \pm 0.10$ ) at  $T_a = 0$  C and highest ( $8.87 \pm 0.64$ ) at  $T_a = 40$  C (Fig. 6b). Little variation exists in rates of EWL at  $T_a$ 's below 20 C (Eq. 6, Table 1). Above  $T_a = 20$  C the rate of EWL increases in a curvilinear fashion (Fig. 6b). Unlike Kansas animals, Texas animals did not salivate excessively when exposed to a  $T_a$  of 40 C for 3-4 hours. Texas animals spread saliva only about the chin and no drooling from the mouth (which was held open) was observed. With Texas animals moisture condensation did not occur in the lines carrying excurrent air. Therefore, EWL



values reported for Texas animals are believed to be accurate estimates. Values of absolute water loss at various  $T_a$ 's are presented in Table 2.

#### Total Conductance

Total conductance was calculated with the following equation:

$$C = \frac{MR}{T_b - T_a}$$

where MR is metabolic rate in ml  $O_2$ /g·h. Values of total conductance (Figs. 7a and 7b) are presented both in units of ml  $O_2$ /g·h·°C and cal/g·h·°C. Caloric conversions (Brody, 1945) were made using an R.Q. of 0.82 (where combustion of 1 ml of  $O_2$  yields 4.825 cal) which was determined to be the average R.Q. for 180 metabolic determinations at various  $T_a$ 's (0-40 C).

#### Kansas animals

Total conductance is minimal and nearly constant at  $T_a$ 's below 25 C (Eq. 7, Table 1; Fig. 7a). Average total conductance at  $T_a$ 's between 0-25 C is  $0.078 \pm 0.004$  ml  $O_2$ /g·h·°C. This average total conductance is 113 % of the value predicted by use of the allometric equation suggested by Bradley and Deavers (1980) for cricetid rodents:  $C = 1.03 W^{-0.54}$ . Above 25 C total conductance increases, with a dramatic increase occurring at  $T_a$ 's above 30 C (Fig. 7a). In tandem with this increase in rate of total conductance is an increase in variability among the responses of individuals, i.e., there is a greater data spread at higher  $T_a$ 's (Fig. 7a). The highest level of total conductance (2.549 ml  $O_2$ /g·h per degree C) was recorded for an individual exposed for 3.5 hours to a

Fig. 7a. Relationship between total conductance in Sigmodon hispidus texianus of Kansas lineage and ambient temperature. Values for total conductance at 40 C are off scale. Caloric conversions based on an R.Q. of 0.82.

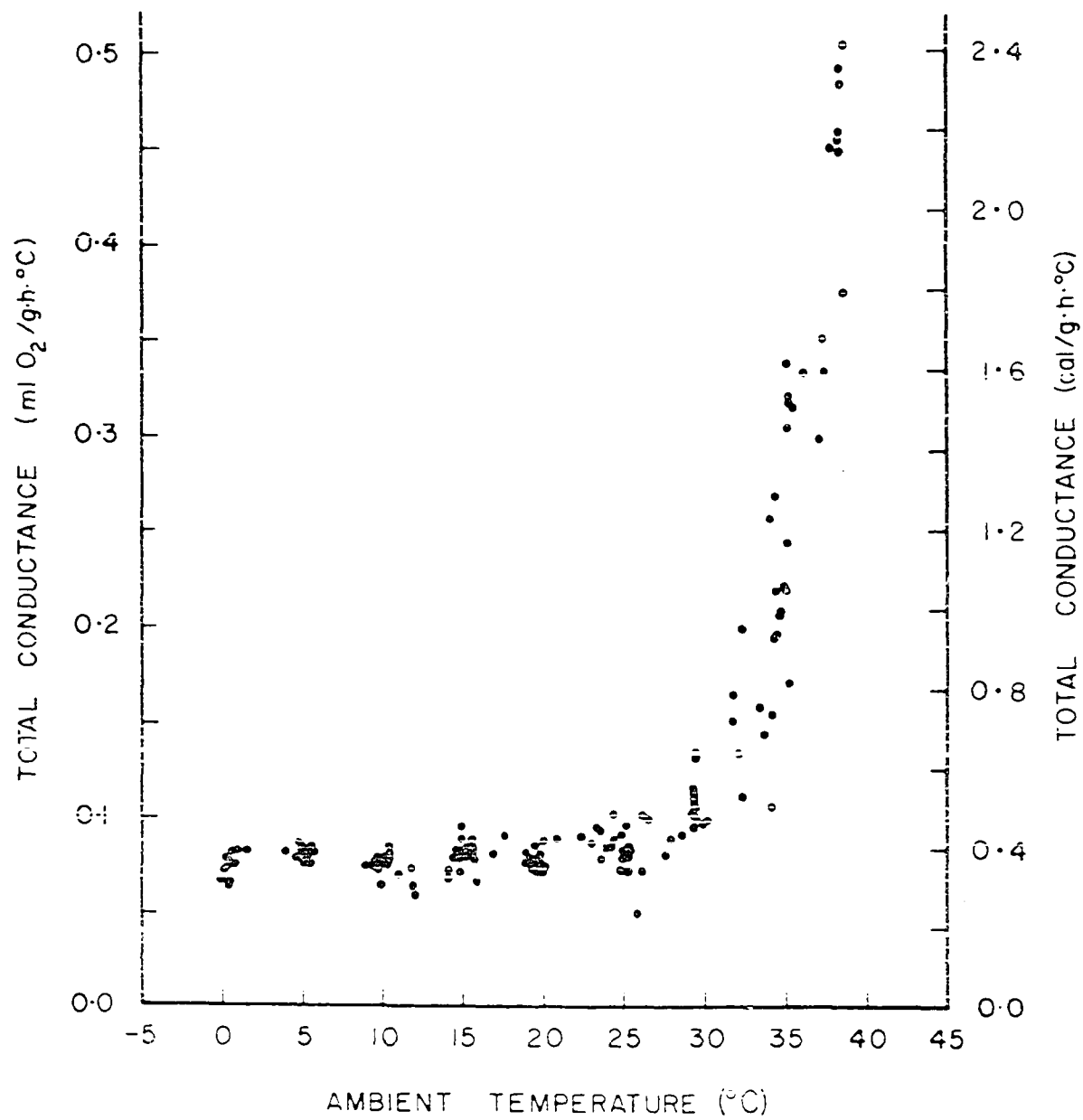
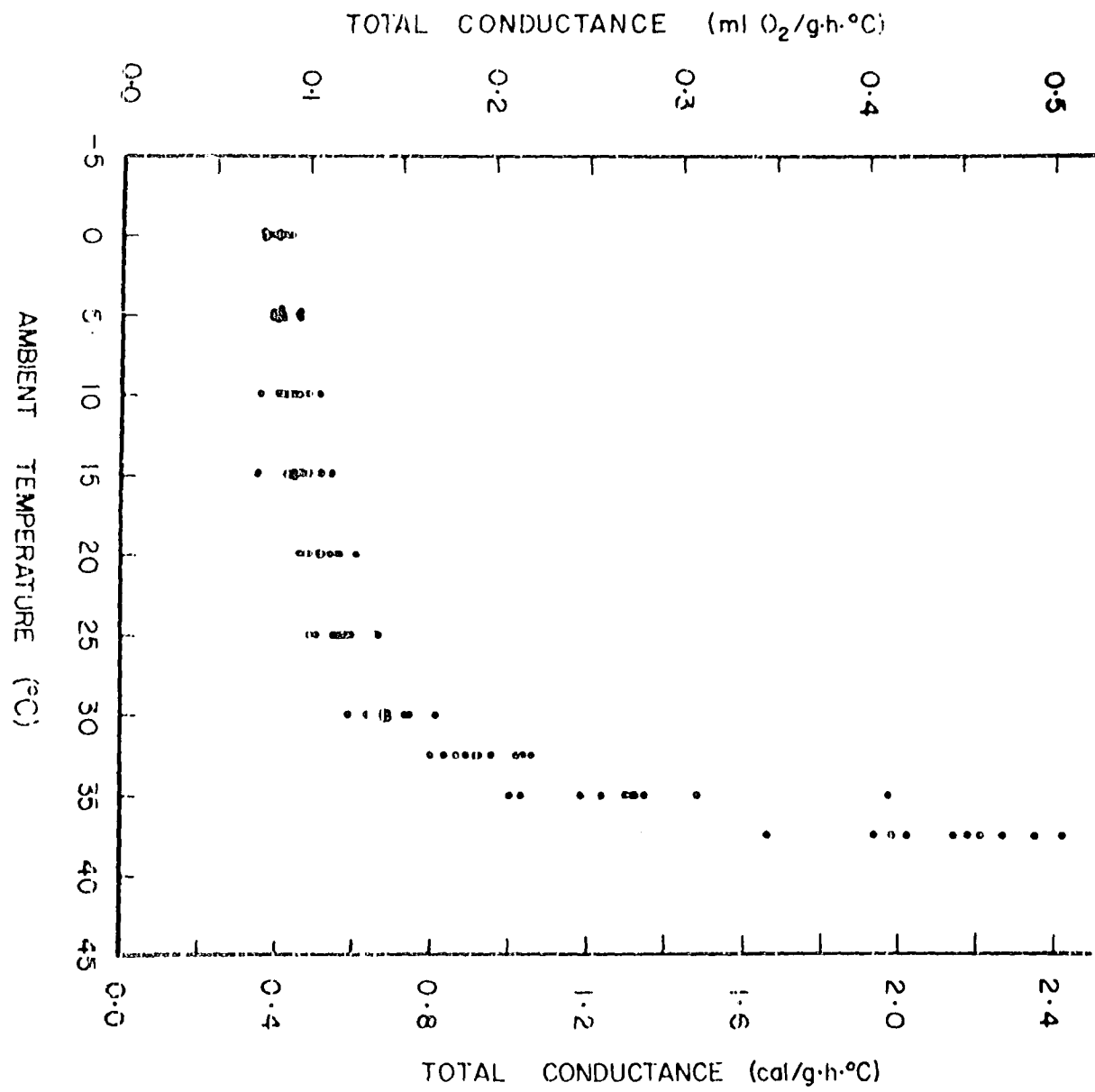


Fig. 7b. Relationship between total conductance in Sigmodon hispidus texianus of Texas lineage and ambient temperature. Values for total conductance at 40 C are off scale. Caloric conversions based on an R.Q. of 0.82.



$T_a$  of 40 C. All data points for total conductance at  $T_a = 40$  C are off the scale of figure 7a ( $1.942 \pm 0.307$  ml  $O_2/g \cdot h \cdot ^\circ C$ , range = 1.057-2.549).

#### Texas animals

Total conductance shows a slight decrease with decreasing  $T_a$  at  $T_a$ 's below 20 C (Eq. 8, Table 1; Fig. 7b). Total conductance is 115 % ( $0.082 \pm 0.002$  ml  $O_2/g \cdot h \cdot ^\circ C$ ) of predicted. (Note: only data from  $T_a = 0$  C are used in this prediction because total conductance at other  $T_a$ 's below thermoneutrality was not minimal and constant.) Above 20 C total conductance increases in a curvilinear fashion with an abrupt increase (and point scatter) occurring at  $T_a$ 's above 32.5 C. The highest rate of total conductance for an individual exposed for 3.5 hours to a  $T_a$  of 40 C was found to be 2.785 ml  $O_2/g \cdot h \cdot ^\circ C$ . As in the case of Kansas animals, all data points for total conductance at  $T_a = 40$  C are off the scale of figure 7b ( $2.062 \pm 0.340$  ml  $O_2/g \cdot h \cdot ^\circ C$ , range = 1.167-2.785).

#### Percent Metabolic Heat Evaporated and Dry Conductance

If it is assumed that evaporation of 1 mg of water dissipates 0.58 cal, the portion of total conductance due to evaporative cooling can be determined (Hudson et al., 1972). When the amount of heat dissipated by evaporative cooling is subtracted from the total conductance, the remainder is the dry conductance (heat loss via convection, conduction and radiation).

### Kansas animals

The percent of metabolic heat lost by evaporation (MHE) is lowest ( $7.3 \pm 1.2$ ) at  $T_a = 0$  C and highest ( $109.7 \pm 8.7$ ) at  $T_a = 39$  C. At  $T_a$ 's below 20 C, MHE increases with increasing  $T_a$  at a relatively slow rate (Eq. 9, Table 1; Fig. 8a). In the 20-30 C range of  $T_a$ 's an abrupt increase in variability in MHE (8.5-40.1 %) can be seen (Fig. 8a). At  $T_a$ 's of 35 C or above (above thermoneutrality) a large increase in MHE and point scatter occurs. The regression line calculated for MHE in the 35-39 C range of  $T_a$ 's (Eq. 10, Table 1) intersects 100 % MHE at a  $T_a$  of 39.5 C.

Dry conductance of Kansas animals exposed to  $T_a$ 's of 0-40 C can be seen in figure 9a. Upon first inspection the plot of dry conductance vs  $T_a$  appears to be quite similar to that of total conductance vs  $T_a$  with simply a reduction (by percentages indicated in figure 8a) in rate of heat loss at any  $T_a$ . However, a very distinct difference can be seen in the conductances in the 30-39 C range of  $T_a$ 's (Figs. 7a and 9a).

### Texas animals

The percent of metabolic heat lost by evaporation is lowest ( $2.4 \pm 0.2$ ) at  $T_a = 0$  C and highest ( $82.1 \pm 10.1$ ) at  $T_a = 40$  C (Fig. 8b). In the  $T_a$  range below 20 C, MHE increases very little with increasing  $T_a$ ; from 2.4 % at  $T_a = 0$  C to 6.5 % at  $T_a = 20$  C (Eq. 11, Table 1; Fig. 8b). Above  $T_a = 20$  C, MHE becomes more variable with large increases in rate of heat loss at the higher  $T_a$ 's (30-40 C). The regression line calculated for MHE in the 35-40 C range of  $T_a$ 's (Eq. 12, Table 1)

Fig. 8a. Percent of metabolic heat evaporated by Sigmodon hispidus texianus of Kansas lineage at different ambient temperatures.



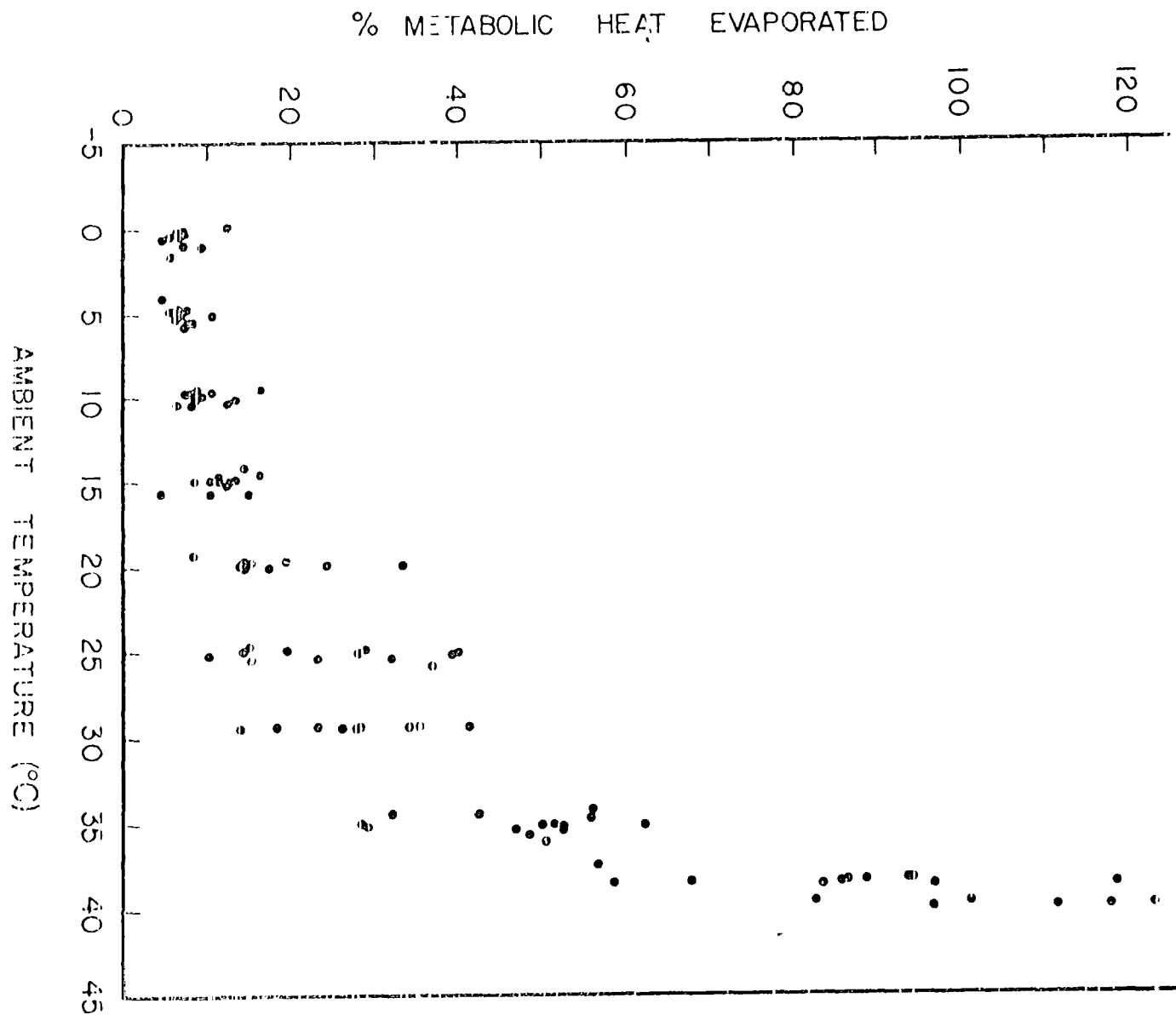


Fig. 8b. Percent of metabolic heat evaporated by Sigmodon hispidus texianus of Texas lineage at different ambient temperatures.

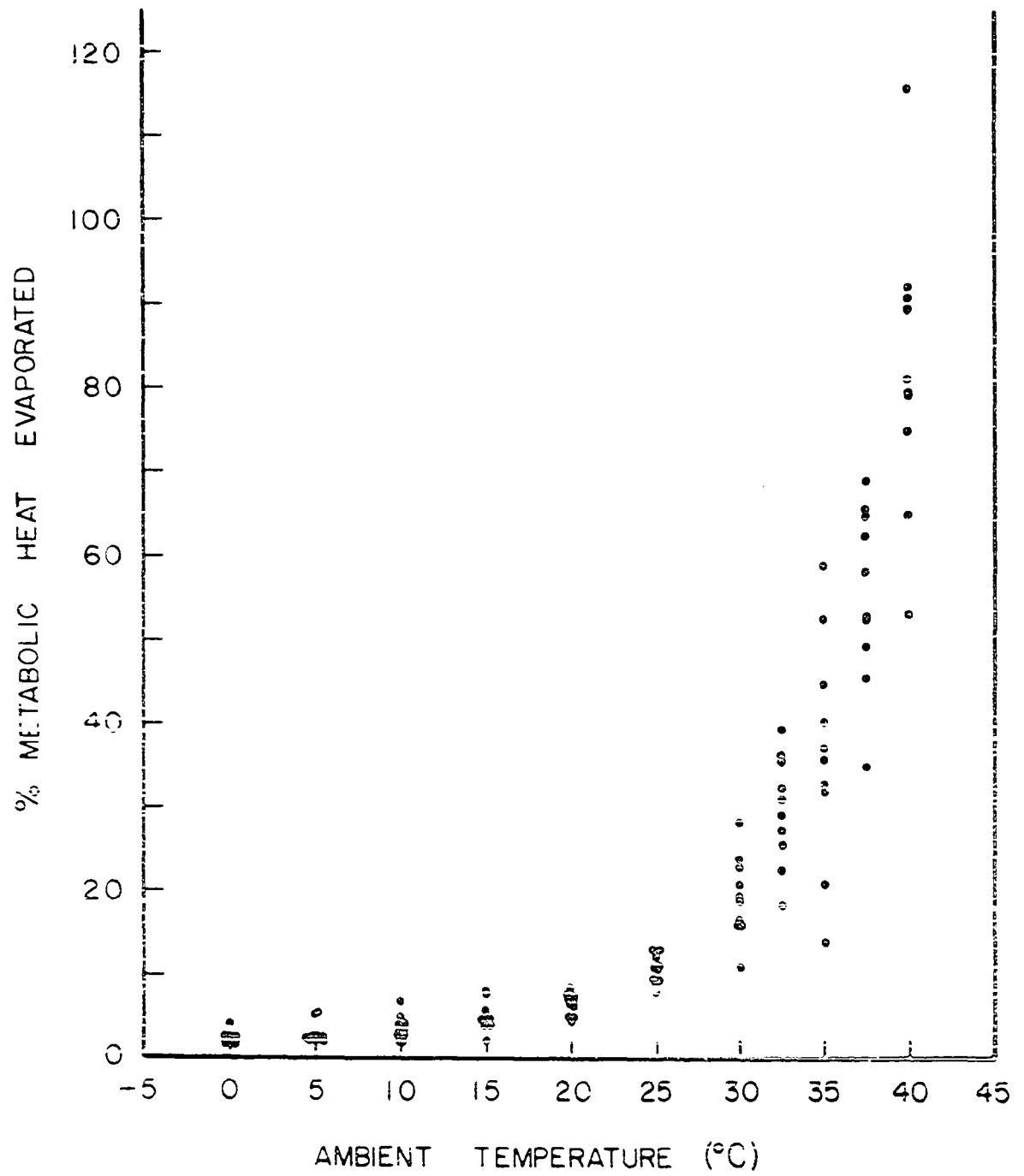


Fig. 9a. Relationship between dry conductance in Sigmodon hispidus texianus of Kansas lineage and ambient temperature. Caloric conversions based on an R.Q. of 0.82.

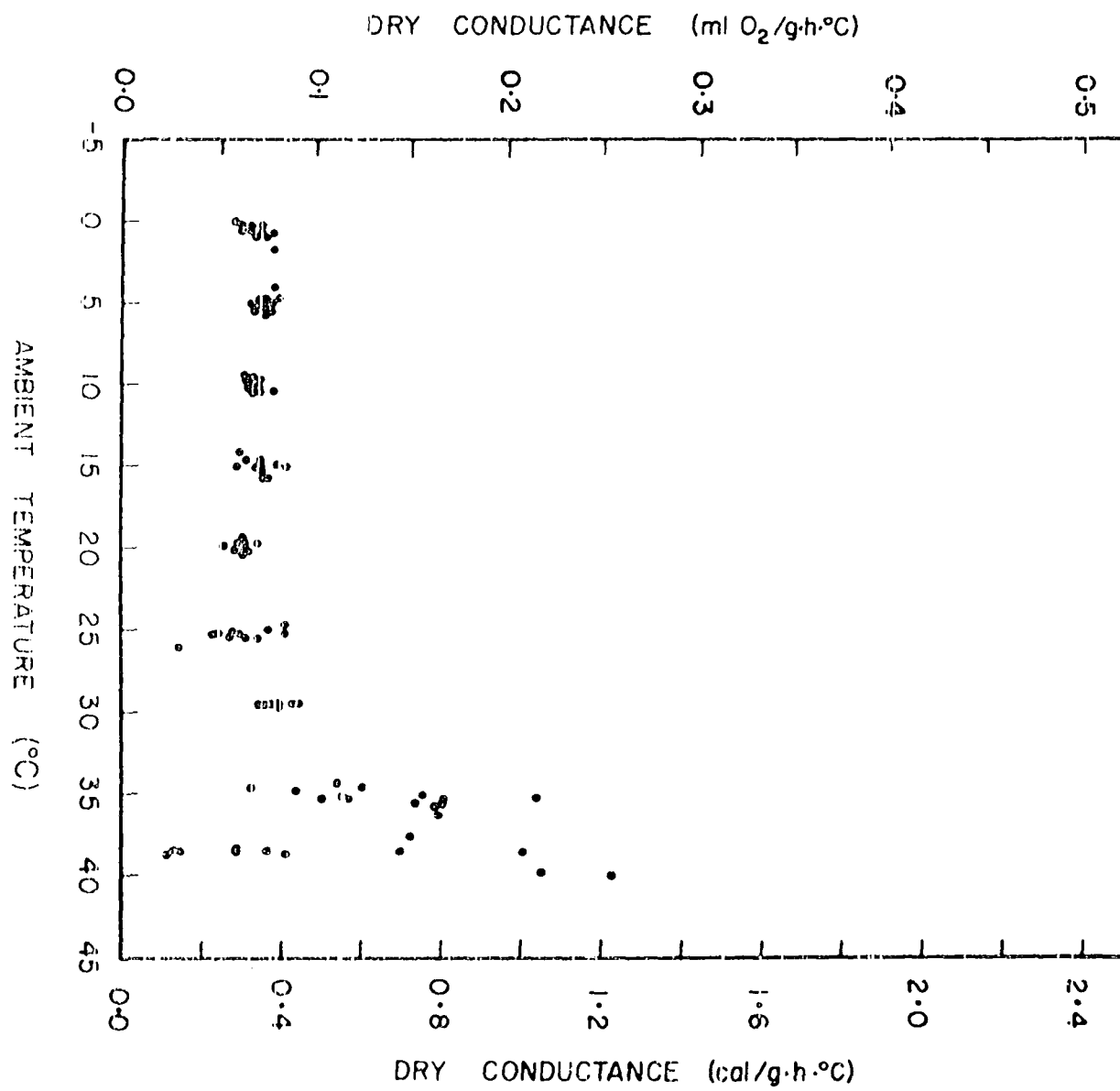
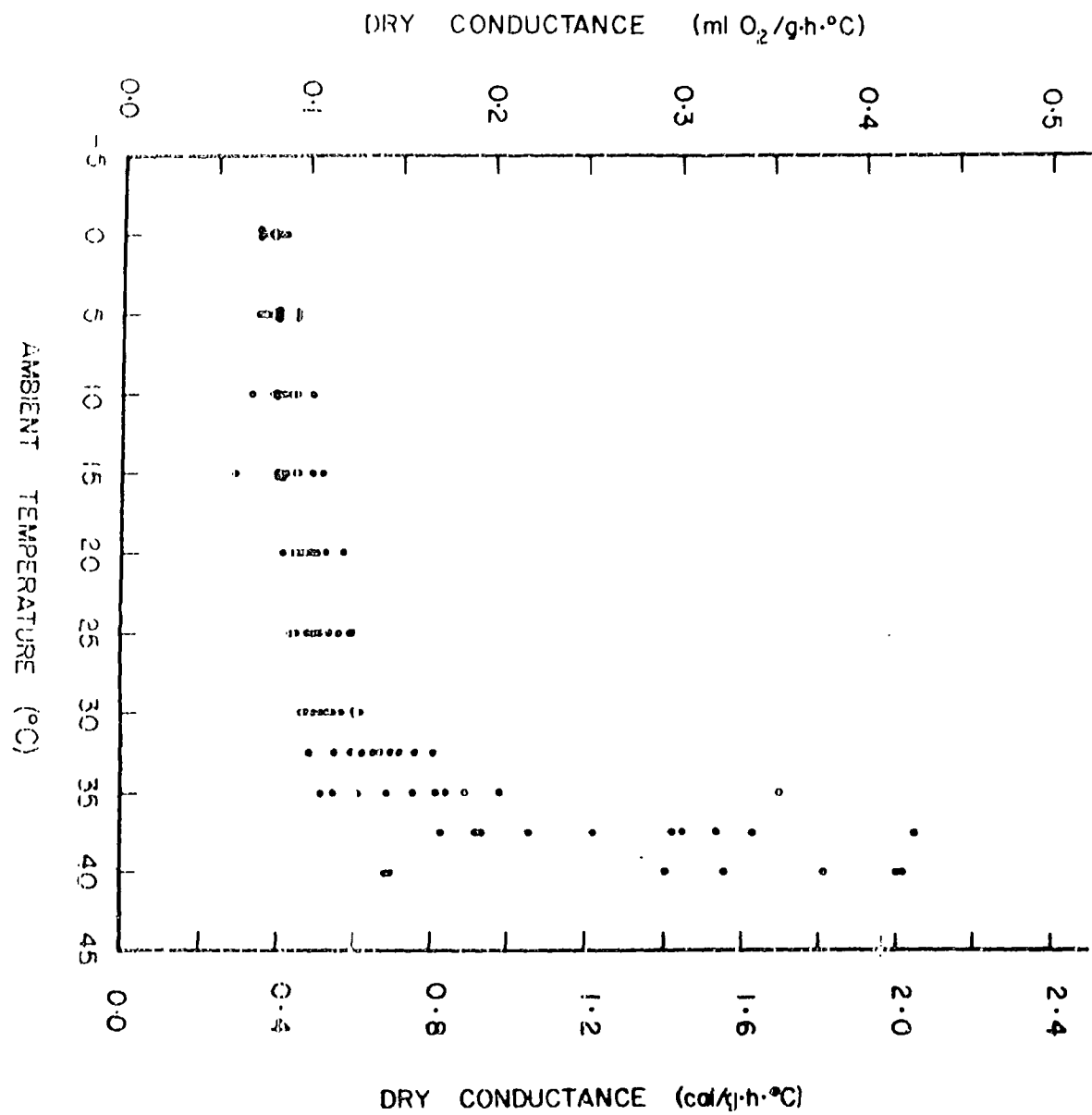


Fig. 9b. Relationship between dry conductance in Sigmodon hispidus texianus of Texas lineage and ambient temperature. Caloric conversions based on an R.Q. of 0.82.



intersects 100 % MHE at a  $T_a$  of 42.8 C.

Dry conductance of Texas animals can be seen in figure 9b. As in the case of Kansas animals, dry conductance does not appear to differ from total conductance (Fig. 7b) to any great extent at the lower  $T_a$ 's. At the higher  $T_a$ 's where EWL plays a greater role in heat dissipation, dry conductance is dramatically different from total conductance. Six of the 10 data points representing dry conductance at  $T_a = 40$  C can be seen in figure 9b whereas none of the 10 data points representing rates of total conductance at  $T_a = 40$  C are low enough to be included in figure 7b.



## DISCUSSION

## Climatic Regime

Kansas animals have body weights approximately 12 grams heavier than Texas animals. This agrees nicely with Bergmann's rule and no doubt is advantageous to animals in the more temperate climate of Kansas. A comparison of the general climatic conditions in northern Kansas and south-central Texas can be found in Table 3.

Table 3. General climatic conditions in northern Kansas and south-central Texas<sup>a</sup>

Index	Kansas	Texas
Average precipitation (cm)		
Annual	16 to 24	80 to 343
January	below 2.5	5 to 10
July	5 to 10	5 to 10
Average annual potential evapotranspiration (cm)	46 to 76	over 137
Average temperature (°C)		
January	-7 to -1	4 to 10
July	21 to 27	27 to 32
Climatic type (Thornthwaite classification)	dry-subhumid	moist-subhumid

<sup>a</sup>Information taken from Muller and Kolenkow (1974).

## Thermoregulation

Thermoneutral zones (TNZ's) determined for Kansas and Texas animals are quite different (Figs. 4a and 4b). The TNZ for Kansas animals (29.5-33.7 C) is closer to that reported by Gaertner (1968) for winter acclimatized Sigmodon hispidus from Arkansas (29.0-33.3 C) than that determined for Texas animals (32.5-35.0 C). On the other hand, basal metabolism in Texas rats (1.03 ml O<sub>2</sub>/g·h) more closely approximates that reported by Gaertner (1968) for spring (0.99), summer (0.94) and fall (1.00) acclimatized cotton rats than does the rate determined for Kansas animals (0.83). Kansas and Texas animals significantly differ in their basal metabolisms (Student t-test,  $P < .01$ ).

No doubt part of the nonconformity as to whether Arkansas animals more closely resemble Texas or Kansas animals (in their thermoregulatory abilities) is probably due to the experimental protocol utilized in Gaertner's (1968) study. Gaertner (1968) reported that food was removed from the cotton rats 2 hours prior to initiation of metabolic determinations. In the present study a minimum of 8 hours of food deprivation was required for Kansas and Texas animals to become post-absorptive (i.e., no specific dynamic action effect). The amount of elevation in metabolic rate due to specific dynamic action may vary from 3-50 % of fasting metabolic rate (Brody, 1945). The amount of variation is dependent not only upon the levels of carbohydrate, fat and protein in the food consumed, but also on the "plane of nutrition" of the animal (i.e., what degree of starvation the animal is in prior to consumption of food), and the  $T_a$  at which the animal is tested (Brody,

1945; Kleiber, 1961). Because of possible specific dynamic action effects it is quite conceivable that the values of basal metabolism reported by Gaertner (1968) actually are closer to the Kansas value than the value determined for Texas animals. Laboratory conditions under which Kansas and Texas animals were maintained more closely reflect summer conditions in northern Arkansas than fall or spring conditions (Arkansas conditions obtained from Muller and Kolenkow, 1974). The average basal metabolic rate for summer acclimatized Arkansas animals is 11 % greater than the rate determined for Kansas animals. If the assumption is made that an average increase in specific dynamic action is approximately 10 % of the basal metabolic rate (Harper, 1975) the rates of basal metabolism are virtually identical.

The TNZ reported for Arkansas animals (Gaertner, 1968) is that of winter acclimatized animals. Ideally, TNZ's determined for Kansas and Texas animals should be compared with the TNZ of summer acclimatized Arkansas animals. Reports of shifts downward in the TNZ (especially the lower critical limit) from summer to winter are common in the literature (e.g., Hart et al., 1965; Hinds, 1977). Gaertner (1968) did not report an upper critical limit for summer acclimatized animals but did report a lower critical limit of 30.0 C which is very close to the lower critical limit of Kansas animals (29.5 C).

Kansas animals have a basal metabolism that is 85 % of that predicted by body weight. The reduction in basal metabolism of Kansas animals is

probably an adaptation for conservation of water in the relatively dry region of the Great Plains from which their ancestors were procured (Table 3). Similar reductions (i.e., approximately 15 %) in basal metabolism have been shown in various small rodents inhabiting xeric regions: Neotoma fuscipes (Lee, 1963), Dipodomys merriami and Dipodomys agilis (Carpenter, 1966), Liomys irroratus (Hudson and Rummel, 1966), and Dipodomys deserti (McNab, 1979). Even larger reductions (20-50 %) in basal metabolism of xeric dwelling rodents have been reported for Perognathus (Tucker, 1965; Chew et al., 1967; Bradley et al., 1975), Liomys salvani (Hudson and Rummel, 1966), Microdipodops pallidus (Brown and Bartholomew, 1969), Peromyscus (McNab and Morrison, 1963), Neotoma (Lee 1963; Nelson and Yousef, 1979) and Spermophilus (Hudson and Deavers, 1973).

Texas animals, on the other hand, have a basal metabolism that is close (103 %) to that predicted by body weight. McNab and Morrison (1963) reported rates of basal metabolism in Peromyscus maniculatus gambeli and Peromyscus truei gilberti close to those predicted by body weight, and they attributed the close agreement between actual and predicted basal metabolisms to the mesic habitats in which the two subspecies are found. Animals inhabiting mesic areas would not have the need for water conservation that animals in more xeric areas would have. Consequently, a reduction in basal metabolism (in mesic dwellers) is not important for survival. Oxygen consumption of Texas animals below thermoneutrality is significantly higher ( $P < .05$ ) than that of Kansas animals (Eqs. 1 and 3, Table 1; Figs. 4a and 4b). Above  $T_a = 35^\circ\text{C}$

rates of oxygen consumption are similar (Eqs. 2 and 4, Table 1; Figs. 4a and 4b).

Total conductance in Texas animals was found to be 115 % of the rate predicted by body weight. Kansas animals had a rate of total conductance that was found to be 113 % of that predicted by weight. In both cases the higher than predicted rates of total conductance do not seem surprising when considering the relatively warm summers in Texas and Kansas (Table 3). A higher than expected level of total conductance would be advantageous for heat dissipation in a warm environment in which only a small amount of radiant heat uptake exists and  $T_b$  is greater than  $T_a$  (McNab and Morrison, 1963; Hudson and Deavers, 1973). Sigmodon hispidus texianus, because of its preference for areas with dense undergrowth (Fleaharty and Mares, 1973; Joule and Cameron, 1975), is not generally exposed to large amounts of intense solar radiation or reradiation from its immediate surroundings. Therefore, higher than predicted ability to dissipate excess endogenous heat via total conductance would be advantageous to the animals during the summer months.

One commonly used method for estimation of total conductance is to statistically fit a line to  $O_2$  consumption below thermoneutrality (as has been done in figures 4a and 4b). The slopes of these lines represent total conductance (Eqs. 1 and 3, Table 1). If the animals tested are "Newtonian animals" (i.e., total conductance and  $T_b$  remain constant below thermoneutrality), the line fitted to  $O_2$  consumption below thermoneutrality will extrapolate to  $T_a = T_b$ . Neither Kansas animals nor Texas animals are "Newtonian animals" (Figs. 4a and 4b); the lines

(of similar slope) extrapolate to  $T_a = T_b$  at 41.6 C and 48.6 C, respectively. Lines (not included in Figs. 4a and 4b) fitted by eye only to the minimal values of  $O_2$  consumption below 20 C in Kansas and Texas animals, extrapolate to 38 C for Kansas animals and 48 C for Texas animals. The  $T_a = T_b$  point obtained by fitting a line by eye to minimal values of  $O_2$  consumption of Kansas animals does reflect a normal  $T_b$  for S. h. texianus. The minimal values of  $O_2$  consumption in Kansas animals obtained at  $T_a$ 's between 20 C and 30 C may not be used for fitting such a line because total conductance does not become minimal and constant until a  $T_a$  of 20 C is approached (Fig. 7a). The line fitted by eye to minimal values of  $O_2$  consumption in Texas animals still does not extrapolate to an acceptable  $T_a = T_b$  point. Actually, in the case of Texas animals no lines can be fitted to minimal values of  $O_2$  consumption (if using more than one  $T_a$  below thermoneutrality) that will extrapolate to a  $T_a = T_b$  point close to the actual  $T_b$  of S. h. texianus. This situation exists because total conductance does not become minimal and constant in Texas animals as  $T_a$  decreases from the lower limit of the TNZ to 0 C (Fig. 7b). Texas animals would need to be subjected to  $T_a$ 's below 0 C before true minimal conductance could positively be predicted. Similar changes in total conductance below thermoneutrality have been reported by several workers including Musser and Shoemaker (1965) for Peromyscus thomasi and Peromyscus megalops and Reinking et al. (1977) for Cynomys ludovicianus. Total conductance (calculated for  $T_a$ 's of 30 C and lower) was determined to be significantly lower ( $P < .01$ ) in Kansas animals than Texas animals at

every  $T_a$  tested (Figs. 7a and 7b). The significantly lower rate of total conductance in Kansas animals at  $T_a$ 's below 30 C probably is the result of a need for heat conservation due to the reduced rate of basal metabolism. Apparently the decrease in total conductance in Kansas animals is sufficient to offset the 15 % reduction in basal metabolism from predicted because the animals are capable of maintaining  $T_b$ 's similar to those of Texas animals at all  $T_a$ 's tested below 30 C (Figs. 5a and 5b). Above  $T_a = 32.5$  C total conductances of Kansas and Texas animals are similar (Figs. 7a and 7b).

#### Heat Loss by Evaporation and Dry Conductance

Kansas and Texas animals did not significantly differ in rates of evaporative water loss (EWL) between  $T_a$ 's of 5-35 C. At  $T_a = 0$  C Texas animals had a rate of EWL that was significantly higher ( $P < .05$ ) than Kansas animals. This difference probably was due to an observed excitability of Texas animals at the low  $T_a$  and represents only an experimental error. At  $T_a$ 's above 35 C Kansas animals have greater difficulty than Texas animals in dissipating endogenous heat. At  $T_a = 40$  C Kansas animals in an attempt to cool themselves by evaporation, spread saliva over the entire ventral portion of the body; especially the highly vascularized regions of the tail and scrotum (if male) and the entire facial area. Texas animals on the other hand, had little difficulty in cooling at  $T_a = 40$  C. Saliva could be seen only about the chin (probably a result of drooling) and the animals did not appear to be stressed as were the Kansas animals. Both Kansas and Texas animals

held the mouth open, possibly to facilitate respiratory EWL across the moist buccal surfaces.

The use of saliva for cooling the body at high  $T_a$ 's has been shown in a number of species of small mammals: e.g., Citellus leucurus (Hudson, 1962), Neotoma fuscipes and Neotoma lepida (Lee, 1963), Dipodomys agilis and Dipodomys merriami (Carpenter, 1966), and Rattus norvegicus (Hainsworth and Stricker, 1970). Hainsworth and Stricker (1970) indicated that not all of the Rattus norvegicus they tested at high  $T_a$ 's spread saliva about the body. Hainsworth and Stricker (1970) concluded that salivation, coupled with spreading saliva about the surface of the body, may be a learned behavior. It is doubtful that this entered into the responses of the Kansas and Texas animals since the animals had never experienced high  $T_a$ 's prior to their exposure to high  $T_a$ 's for metabolic determinations.

Rates of EWL at  $T_a = 40^\circ\text{C}$  do not appear to differ between Kansas and Texas animals (Figs. 6a and 6b). However, as previously mentioned, rates of EWL for Kansas animals are conservative approximations at best (due to the moisture condensation in the excurrent air line). Extreme care was required to ensure that rates of EWL were not measured when animals were active (even mildly active) because EWL would greatly increase during activity. This is in agreement with previous reports on increased rate of EWL with activity (see Christian, 1978).

The importance of evaporative cooling to total conductance is significantly greater ( $P < .01$ ) in Kansas animals than in Texas animals at  $T_a$ 's between 0-30  $^\circ\text{C}$  (Figs. 8a and 8b). No significant difference in



percent metabolic heat evaporated could be shown at  $T_a = 35^\circ\text{C}$  although Texas animals generally have values lower than Kansas animals. At  $T_a = 39\text{--}40^\circ\text{C}$  Kansas animals do have a significantly ( $P < .01$ ) greater amount of heat lost by evaporation than do Texas animals. Regression lines calculated for percent metabolic heat evaporated between  $T_a$ 's of  $35$  to  $39\text{--}40^\circ\text{C}$  indicate that Kansas animals evaporate 100 % of their metabolic heat production at  $T_a = 39.49^\circ\text{C}$ , whereas Texas rats would have evaporated 100 % of their metabolic heat only if the  $T_a$  had been raised to  $42.76^\circ\text{C}$ .

When evaporative heat loss is subtracted from the total conductance the value remaining, dry conductance, represents the amount of heat that is dissipated by conduction, convection and radiation. Thus, the less well-insulated an animal is the greater will be its dry conductance. Dry conductance was found to be significantly higher ( $P < .01$ ) in Texas animals than in Kansas animals at all  $T_a$ 's tested (except  $35^\circ\text{C}$ ). As previously mentioned for differences in total conductance between Kansas and Texas animals, the reduction of dry conductance in Kansas animals is probably in response to a need for conservation of endogenous heat (due to a reduced basal metabolism) for maintenance of body temperature at cooler environmental temperatures. This reduction in dry conductance (compared to Texas animals) does pose a disadvantage for Kansas animals at high  $T_a$ 's. Kansas animals obviously cannot cool themselves at  $40^\circ\text{C}$  without excessive salivation. In nature, such excessive salivation would hinder the ability of Kansas animals to conserve water during periods of high environmental temperatures. Kansas animals avoid exposure to high

environmental temperatures (by being most active at night, remaining in shaded areas, etc.) so that this problem for the most part, is non-existent. Texas animals do not appear to have any difficulty in thermoregulating at the higher  $T_a$ 's tested in this study. Most likely the significantly higher rate of dry conductance in Texas animals than in Kansas animals enables the Texas animals to cope with high environmental temperatures with little apparent difficulty. Significant difference in dry conductance could not be shown between Texas and Kansas animals at  $T_a = 35$  C due to the large degree of variability (and overlap) in the responses within the two groups (Figs. 7a and 7b, 8a and 8b). Dry conductances at  $T_a$ 's between 35 to 39-40 C were about 20-25 % of total conductances in both Texas and Kansas animals which is similar to that reported by Hudson and Deavers (1973) for six species of ground squirrels.

### Conclusion

The data presented indicate that Kansas animals are genetically distinct from Texas animals in their thermoregulatory abilities. In the process of northward migration into dryer and cooler regions of the Great Plains, individuals possessing the traits for lowered basal metabolism and reduced total and dry conductances have been selected for by evolutionary processes. These traits enable animals to conserve water which may be in short supply during the dryer and warmer periods of the year while maintaining  $T_b$  at a level similar to that found in animals at the southern end of the distribution of the subspecies.

These adaptations have secondarily permitted animals in the northern regions of the distribution to more efficiently thermoregulate at low environmental temperatures (-7 to -1 C) during winter. The reduction in thermal conductance (total and dry) enables Kansas animals to conserve significantly more endogenous heat than Texas animals and thus, maintain normothermic  $T_b$ 's at a lower metabolic cost. At  $T_a = 0$  C Kansas animals are able to maintain similar  $T_b$ 's to those of Texas animals for only 88 % of the metabolic cost, and this savings increases as  $T_a$  approaches thermoneutrality. No doubt a metabolic savings of 12 % (or more) prorated over an entire winter season in Kansas may be of extreme importance for survival, especially when food and water may be in short supply and difficult to procure (Fleharty et al., 1972).

Winters in northern Kansas are extremely harsh compared to winters in south-central Texas. Populations of Sigmodon hispidus texianus typically undergo large reductions in numbers or total local extinction due to lack of sufficient food availability and cold environmental temperatures (Fleharty et al., 1972). It is my belief that the original adaptive advantages of reduced basal metabolism and thermal conductances for conservation of water probably are overshadowed in the more northern populations by the advantages of heat conservation and food conservation during winter. Such abilities would permit animals to withstand periods of extremely bitter cold during winter (either by foraging for needed food resources during these times or surviving longer periods of cold weather starvation between feedings), thereby ensuring survival of the species in the more northern latitudes.

DEVELOPMENT OF THERMOREGULATION IN THE NEONATAL  
HISPID COTTON RAT, SIGMODON HISPIDUS TEXIANUS,  
FROM NORTHERN KANSAS AND SOUTH-CENTRAL TEXAS

## INTRODUCTION

In the previous section, I reported that phylogenetic differences existed in the metabolism of laboratory-reared adult Sigmodon hispidus texianus from northern Kansas and south-central Texas. It was found that at ambient temperatures of 0-40 C adults from Kansas lineages had lower rates of thermal conductance and oxygen consumption than their southern counterparts. I hypothesized (section I, herein) that the lower rates of thermal conductance and oxygen consumption found in Kansas animals might be advantageous to populations of S. h. texianus that have moved northward (within the past century) into more temperate and xeric regions of North America. Reviews of the considerable documentation on this northward movement of S. h. texianus can be found in Cockrum (1948) and Genoways and Schlitter (1966). Lower rates of thermal conductance and metabolism would seem to be especially advantageous for survival of the harsher winters in the more northern latitudes (37-40°N lat.). Fleharty et al. (1972) indicated that the stress imposed upon S. h. texianus by exposure to severe cold weather is probably the primary factor in determination of the northern boundary for the distribution of this species.

Several studies have looked at latitudinal differences in reproduction and postnatal development of S. h. texianus (Kilgore, 1970; Bowdre, 1971; McClellaghan and Gaines, 1978). However, these studies have not examined the postnatal development of thermoregulation. Numerous studies have been conducted on the development of thermoregulation in small rodents (Table 4); but, none of these studies have looked at possible

latitudinal differences in this development.

Table 4. Selected listing of studies on development of thermoregulation in small rodents

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gerbil	McManus, 1971
ground squirrel	Maxwell and Morton, 1975 Dolman, 1980
guinea pig	Bruck and Wunnenberg, 1966
hamster	Hissa, 1968
lemming	Hissa, 1968
vole	Morrison <u>et al.</u> , 1954
mice	Fitzgerald, 1953 Chew and Spencer, 1967 Hill, 1976
rabbit	Hull and Segall, 1965a,b
rat	Hahn <u>et al.</u> , 1956 Taylor, 1960 Takano <u>et al.</u> , 1979

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Therefore, the purpose of this study was to: 1) examine the development of thermoregulation in laboratory-reared neonatal S. h. texianus of Kansas and Texas lineages and 2) determine if differences in thermal conductance and metabolic rate exist between neonatal S. h. texianus of Kansas and Texas lineages (as have been shown to exist in the adult).

## METHODS AND MATERIALS

## Experimental Animals

Adult specimens of Sigmodon hispidus texianus were obtained from localities near College Station, Texas and Hays, Kansas. These localities are representative of the southern and northern regions inhabited by this subspecies. Within 2 weeks of capture, animals were shipped via air to Iowa State University, the site of this study.

Animals were maintained on a 14L:10D photoperiod at  $23 \pm 2^\circ\text{C}$  which has previously been reported as an optimal condition for the breeding of cotton rats in captivity (Meyer and Meyer, 1944; Johnston and Zucker, 1979). Food (Teklad 4 % Mouse & Rat Chow) was available only during the dark phase of the photoperiod cycle to ensure that animals did not become obese. Food was available ad libitum to lactating females. Water was available ad libitum to all animals.

Twenty-four wild-caught animals from Texas and 23 wild-caught animals from Kansas were used for establishment of an  $F_1$  breeding colony. All neonates used in this study were offspring of  $F_1$  adults. Inbreeding was avoided and animals of Texas and Kansas lineages were never interbred.

Males and females were paired and housed in 45 x 25 x 20 cm cages. Wood shavings and paper towels were provided for bedding and nesting materials, respectively. Males were removed from cages shortly prior to or no longer than 12 hours after birth of young. Randolph et al. (1977) reported that the young of S. hispidus were typically born on night 26 or day 27 of gestation. Seventy-eight of 81  $F_2$  litters

used in this study were born at night; the remainder were born in late afternoon. Although actual gestation periods were not determined, 2 females in which postpartum mating occurred gave birth to subsequent litters 27 days after delivery of the first litter. Cages were checked at 12 hour intervals, therefore, ages of litters could be accurately determined to within 12 hours.

All experiments were performed during the light phase of the photoperiod cycle. Females were separated from their litters with a piece of cardboard when neonates were required for experimentation. After experimentation, neonates were returned to their mothers which normally accepted them. However, to prevent rejection, 1- to 2-day-old neonates exposed to cold temperatures had to be artificially rewarmed prior to replacement in the nest. Litters were permanently taken from their mothers at 21 days of age. At that time all neonates were examined and weighed to determine if tested siblings had comparable morphological development to untested siblings. Neonates were identified by toe clipping.

#### Tests on Individual Young

In these tests, young of ages 1-18 days were subjected, individually, to ambient temperatures ( $T_a$ 's) of 0-35 C for 3-3.5 hours. Ambient temperatures were selected at 5 C increments. Each neonate was subjected to only one  $T_a$  on a given day. Most animals were tested twice during this 18 day period. In these cases a minimum of 7 days transpired before the animals were tested the second time. Also, the second test was carried out at a  $T_a$  that differed by at least 15 C from the  $T_a$



of the first test. Only one sibling per litter was tested on a given day and every effort was made to test other siblings at different  $T_a$ 's. This aided in reduction of possible bias introduced by any litter; especially at the lower  $T_a$ 's. Litters of more than 10 or less than 4 were not used for experimentation due to the atypical large or small size of the individuals, respectively. Likewise, if litters included a "runt," the animal was not used but was permitted to remain with the litter. The sex ratio was approximately equal.

Tests involved placement of an animal in a metabolism chamber at the selected  $T_a$ . Metabolism chambers of three different sizes were used. The chambers were fashioned from 0.47 liter (for 1- to 5-day-olds), 1.5 liter (for 6- to 10-day-olds) and 4.7 liter (for 11- to 18-day-olds) paint cans. For each chamber, a wire mesh platform was placed 3 cm above the floor of the chamber for the animals to rest upon. A layer of paraffin oil was placed on the bottom of each chamber to prevent evaporation of moisture from urine and feces eliminated by the animal during experimentation. Openings in the lid of each chamber permitted placement of incurrent and excurrent ducts for air and a YSI temperature probe for measurement of chamber temperature.

Prior to introduction of the animal, the metabolism chamber was heated or cooled to the  $T_a$  selected for experimentation. After introduction of the animal, the chamber was sealed and placed in a Precision Instruments Model 815 low temperature incubator. The internal temperature of the chamber was maintained at  $\pm 0.1^\circ\text{C}$  of desired temperature.

Oxygen consumption of the animal was determined by open system respirometry (Depocas and Hart, 1957). Compressed air was passed through a column of silica gel (to remove moisture), regulated to a flow of 500 ml/min (200 ml/min for 1-day-olds) with a factory calibrated Brooks 110 flowmeter and passed through the sealed metabolism chamber. Excurrent air was passed through trains of silica gel and Ascarite (to remove  $\text{CO}_2$ ). A portion of the dry,  $\text{CO}_2$ -free excurrent air was diverted to an oxygen analyzer (Applied Electrochemistry S-3A) for continuous measurement of oxygen content. Output from the oxygen analyzer was recorded by a Houston Instruments strip chart recorder.

At the end of 3 hours in the metabolism chamber, water from pulmocutaneous evaporation was collected for approximately 25 minutes in a pre-weighed column of silica gel. Change in weight of the column was determined to the nearest 0.1 mg on a Mettler H33 balance. If the animal became active during the period of collection, the value obtained was discarded. The mean oxygen consumption reported for each test was obtained by planimetry (Keuffel & Esser Co.) from the final 15 minutes of this collection period. Oxygen consumption was generally stable within the 15 minute measurement period except at low  $T_a$ /1- to 6-day-old neonate combinations. In those cases there was generally a steady decline throughout the 15 minute period. Oxygen consumption reported for all instances is an average for the final 15 minute period of water collection.

Body temperature was taken at the beginning and within 30 seconds of the end of each test with a 30-gage copper-constantan thermocouple

probe inserted 1-2.5 cm into the rectum. The probe was coated with a thin layer of Insulex and connected to a Pederson 37MR recording potentiometer. Body weights were determined prior to and after the 3.5 hour test period.

Tests were repeated a minimum of 3 times for each age/temperature combination.

#### Tests on Litters

In these experiments 4 siblings, chosen at random if litters were larger than 4, were exposed for 3.5 hours to 0 C. The litters were tested while in a cotton nest with walls approximately 2 cm thick. The nest totally surrounded the litter and was enclosed in a wire mesh cage to inhibit movement from the nest. The experimental procedures for testing litters were similar to those previously described for testing individuals with the following exceptions: (1) the metabolism chamber was 11.4 liters in size, (2) air flow was increased to 1200 ml/min, (3) no water from pulmocutaneous water loss was measured and (4) body temperatures were measured in 2 of the 4 siblings. Each litter was tested on 2 different occasions. Again, as in the case of multiple tests on a given individual, a minimum of 7 days was permitted to pass prior to the second test.

#### Detection of Shivering

Tests were conducted to determine the age of onset of visible shivering thermogenesis. Neonates 1 to 7 days of age were placed individually on the floor of a container covered with a 1 cm layer

of sawdust. The container was placed in a walk-in cooler maintained at  $5 \pm 1$  C. Individuals were observed for 3 minutes (or until shivering commenced) to ascertain whether visible shivering was exhibited. Each individual was tested daily until visible shivering was noted.

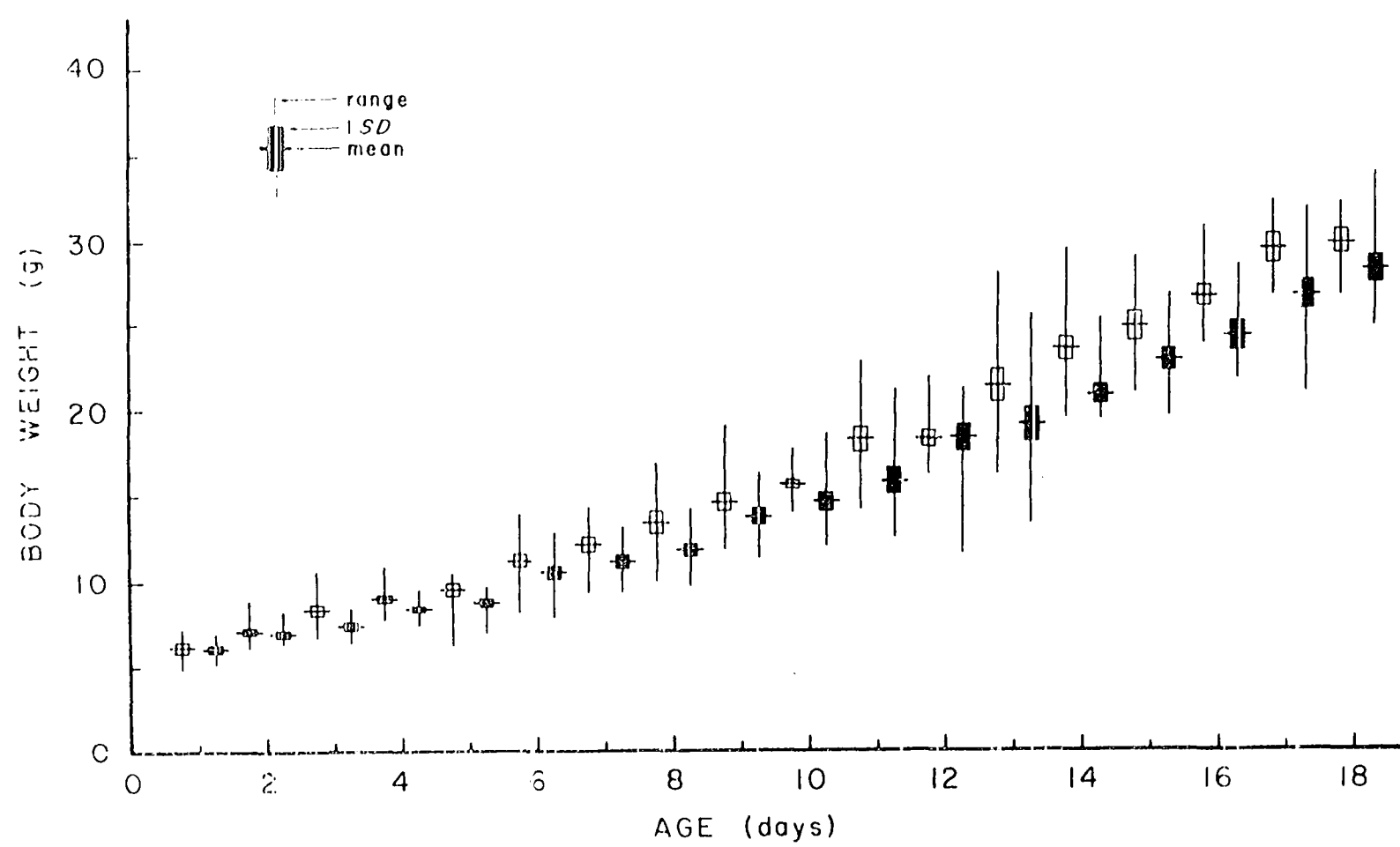
## RESULTS

## Anatomical Development

A comparison of growth rates in randomly selected neonates of Kansas and Texas lineages (10 for each lineage-age combination) can be seen in figure 10. Average weights and standard deviations of 1-day-old Kansas and Texas neonates are very similar; Kansas:  $6.3 \pm 0.82$  grams, Texas:  $6.19 \pm 0.58$  grams. A significant difference (Student t-test,  $P < .05$ ) in weight develops in animals older than 4 days of age (Fig. 10). Generally, at any given age except days 1 and 2, Kansas neonates are approximately 5-11% heavier than Texas neonates. Variation in absolute weight is greatest in 6- to 17-day-old Kansas and Texas neonates. Variations in weight expressed as coefficients of variation are greatest in Texas neonates between days 6-17 (11.1 to 17.4 %) and greatest in Kansas neonates during the 1- to 14-day-old period (11.5 to 15.2 %). Average coefficients of variation for the entire growth period (1-18 days) are 11.7 % and 12.5 % for Kansas and Texas neonates, respectively.

In both Kansas and Texas neonates, the growth curves appear to be triphasic (Fig. 10). Weight gains as grams/day for the first growth phase (days 1-5) are 0.94 and 0.74 grams for Kansas and Texas neonates, respectively. Weight gains for the second growth phase (days 6-10) are 1.14 and 1.19 grams for Kansas and Texas neonates, respectively. The third growth phase (days 10-18) is represented by weight gains of 1.84 and 1.68 grams for Kansas and Texas neonates, respectively.

Fig. 10. Relationship of body weight with age in randomly selected neonatal Sigmodon hispidus texianus of Kansas lineage (open bars) and Texas lineage (solid bars).



Postnatal anatomical development is similar in both Kansas and Texas neonates. One- and 2-day-old neonates are naked on the belly and chin but have short hair on the dorsal surface. The hair on the dorsal surface does not totally obscure the skin. Three- and 4-day-old neonates have longer, thicker hair dorsally which completely obscures the skin. Ventrally, a thin layer of fur develops by the 3rd or 4th day. From days 5 to 7 the dorsal and ventral fur becomes visibly thicker and much longer. Eighteen-day-old neonates resemble adults in pelage characteristics except for a less dense coat of fur on the medial surfaces of the appendages of neonates.

The eyes typically open on the second day of life. A few animals opened their eyes on the first day (2 %) and third day (10 %). All animals have opened their eyes by the third day after birth. Eruption of the teeth also occurred in all animals by the third day. Ten-day-old animals were commonly observed to eat rat chow provided for the mother. On day 12, a change in temperament was noted in most neonates; i.e., neonates began to nip when handled. This behavior was never observed in neonates prior to day 12.

#### Development of Thermoregulation in Individuals

Body temperature ( $T_b$ ), rate of  $O_2$  consumption and total conductance in the individual neonate is indistinguishable between Kansas and Texas neonates; therefore, the data are pooled. Results for  $T_b$  and associated rate of  $O_2$  consumption and total conductance for 1- to 18-day-old individuals exposed for 3.5 hours to ambient temperatures of 0-35 °C



Fig. 11. Relationship of final body temperature after 3.5 hr exposure to various ambient temperatures for the 1st to 18th days of life in Sigmodon hispidus texianus of Kansas lineage (open circles) and Texas lineage (solid circles). Data are not included for animals which failed to survive the test period.

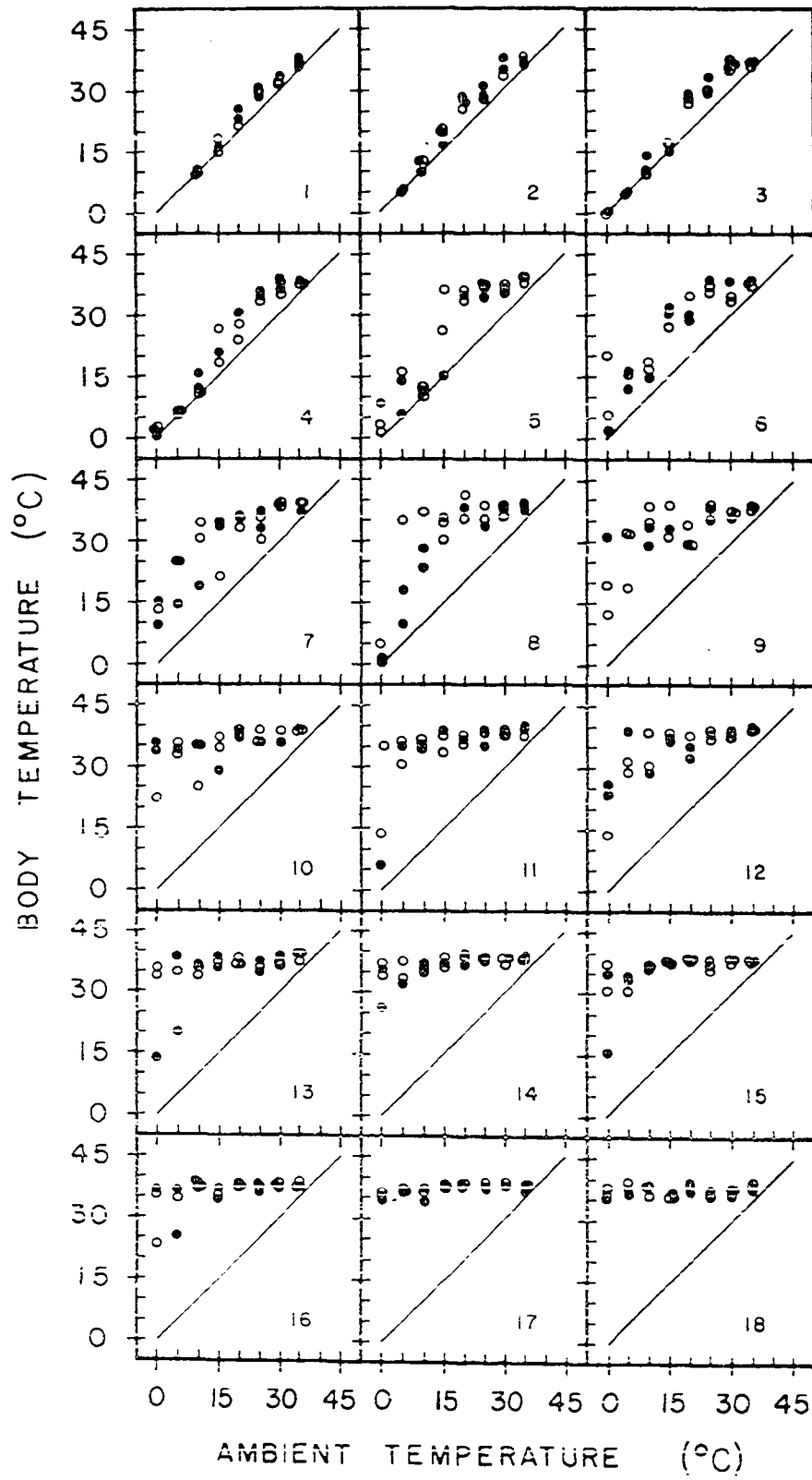


Fig. 12. Relationship of  $O_2$  consumption after 3 hr exposure to various ambient temperatures for the 1st to 18th days of life in Sigmodon hispidus texianus of Kansas lineage (open circles) and Texas lineage (solid circles). Data not included for animals which failed to survive the test periods. Animals which had metabolic rates too low to detect are represented as having zero  $O_2$  consumption.

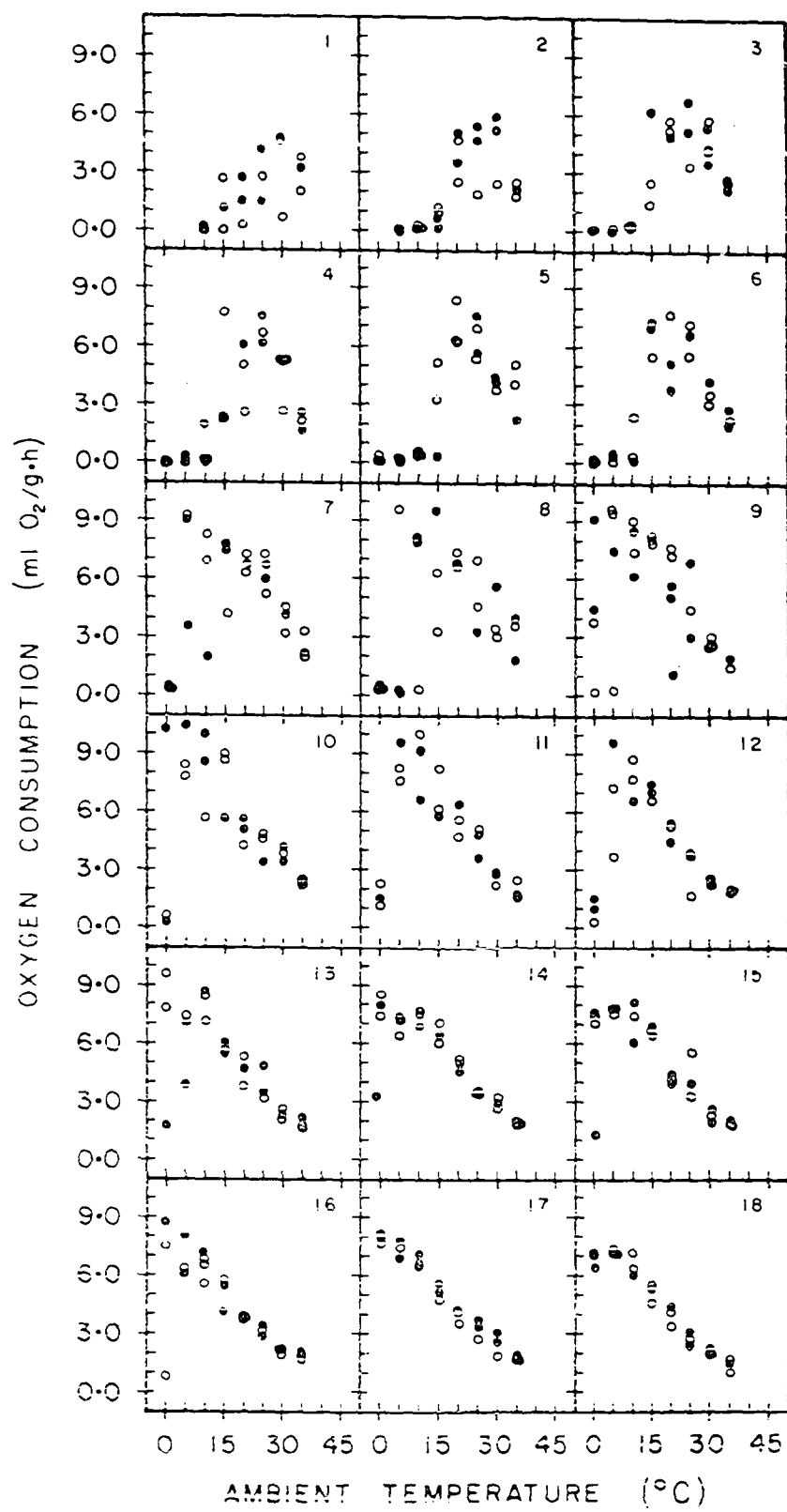
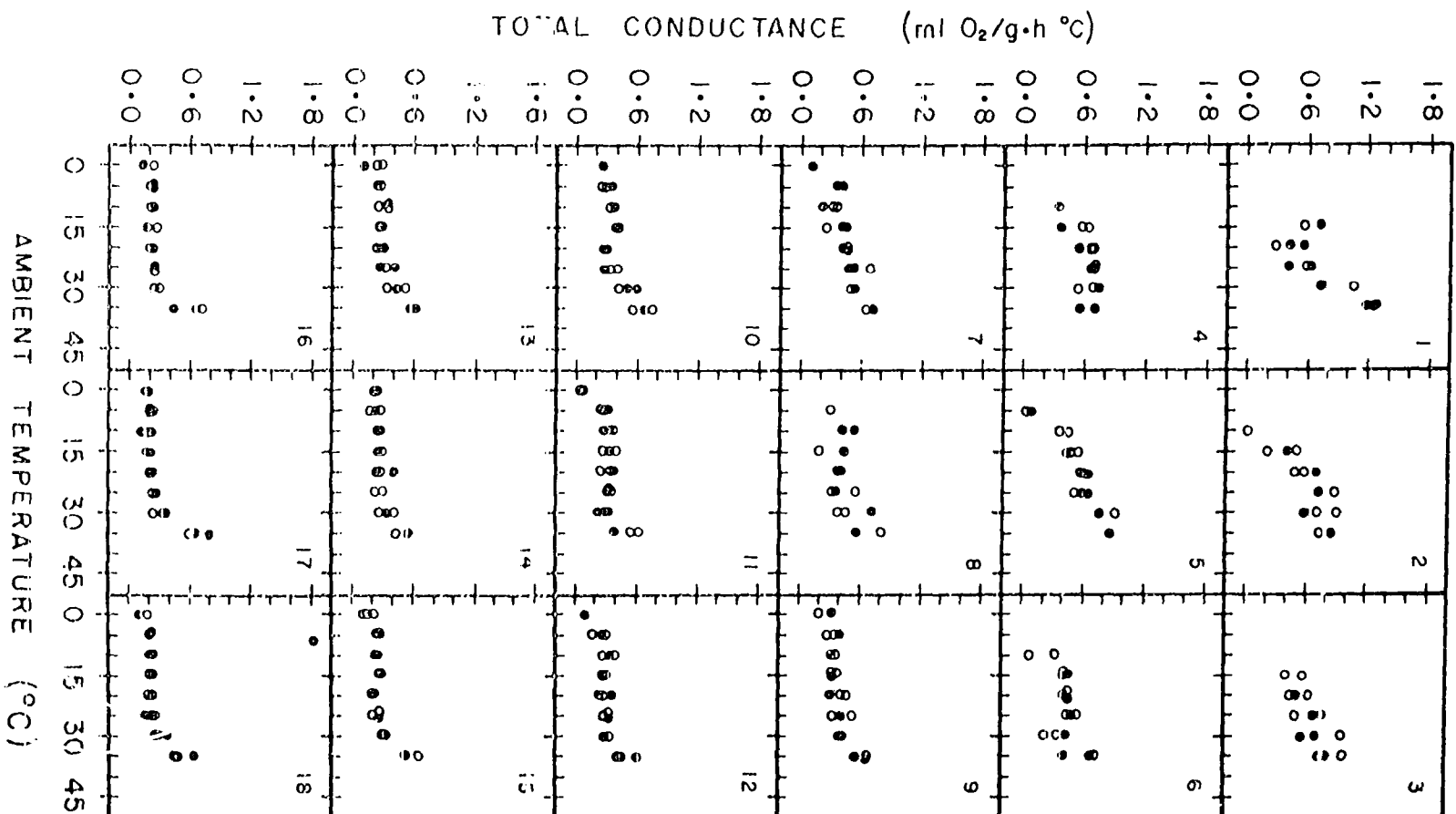


Fig. 13. Relationship of total conductance after 3 hr exposure to various ambient temperatures for the 1st to 18th days of life in Sigmodon hispidus texianus of Kansas lineage (open circles) and Texas lineage (solid circles). Data not included for animals which failed to survive the test periods or had metabolic rates too low to detect.



can be seen in figures 11, 12 and 13, respectively.

### Body temperature

One-day-old neonates are essentially poikilothermic in their response to various ambient temperatures. Final  $T_b$  is maintained 2-3 C above ambient temperature ( $T_a$ ) in the 15-35 C range of  $T_a$ 's (Fig. 11). Below  $T_a = 15$  C  $T_b$  drops to the level of the  $T_a$  at which the neonate is tested. One individual tested at 10 C and all individuals tested at 5 C and 0 C failed to survive the 3.5 hour test period. (Data for these instances and any similar instances on any other day are not included in figures 11, 12 and 13.) Plots of  $T_b$  vs  $T_a$  for days 2-3 indicate a greater ability to maintain  $T_b$  1-3 C above  $T_a$  in the 15-30 C range of  $T_a$ 's. On day 2 one animal tested at 5 C and 2 animals tested at 0 C failed to survive test periods. One individual each at  $T_a$ 's of 0 C and 5 C failed to survive test periods on day 3. Plots for days 4-6 show a progressive increase in ability of the individual to maintain its  $T_b$  up to 11 C above  $T_a$  but animals still are limited in this ability at  $T_a$ 's below 15 C.

Homeothermic capability in 1- to 7-day-olds at  $T_a$ 's below 35 C appears to be more closely related to age than to body weight. For example, a 3-day-old neonate weighing 10 grams, if tested at  $T_a$ 's below thermoneutrality, typically will have a final  $T_b$  that is lower than the final  $T_b$  of a 4-day-old neonate weighing 8 grams. For  $T_a$ 's above 30 C this is not true.

Plots of final  $T_b$ 's for days 7-9 show a further increase in ability to maintain a stable  $T_b$  at all  $T_a$ 's although considerable variation does

exist among individuals in this ability. This variation is especially noticeable at  $T_a$ 's below 25 C (Fig. 11). On day 9, the lowest  $T_b$  recorded was 12 C above  $T_a$  (0 C). On days 10-12, a further refinement of homeothermy can be seen with large individual variations occurring only in the 0-15 C range of  $T_a$ 's (Fig. 11). By day 13, Sigmodon hispidus appears to be essentially homeothermic ( $T_b = 32-38$  C) throughout the 0-35 C range of  $T_a$ 's. Plots of  $T_b$  vs  $T_a$  for days 13-16 are basically uniform: a stable  $T_b$  at  $T_a$ 's above 5 C with some fluctuation in  $T_b$  at  $T_a$ 's of 0 C and 5 C. By day 17,  $T_b$  is consistently maintained ( $T_b = 35-38$  C) at all  $T_a$ 's.

#### Oxygen consumption

All individuals exhibited some capability for endothermy at all  $T_a$ 's tested. One- to 6-day-old animals, especially at low  $T_a$ 's, could not maintain stable rates of  $O_2$  consumption throughout the 3.5 hour test period. As previously mentioned, several animals 1-3 days of age were incapable of surviving tests at low  $T_a$ 's (0-10 C). Again, data for these instances are not included in figure 12. Neonates that survived the test period but had rates of  $O_2$  consumption too low to detect are noted as having zero  $O_2$  consumption (Fig. 12). Oxygen consumption in one-day-olds is highest at the higher  $T_a$ 's with a tremendous amount of variation in rates at any given  $T_a$  (e.g., at  $T_a = 30$  C, values of  $O_2$  consumption range between 0.5-5.0 ml  $O_2$ /g·h). As animals mature (days 2-6), plots of the rates of  $O_2$  consumption vs  $T_a$  (Fig. 12) are somewhat bell-shaped with the highest rates occurring in the 15-25 C range of  $T_a$ 's and lowest in the 0-15 C and 30-35 C ranges of  $T_a$ 's. From days 6-12,



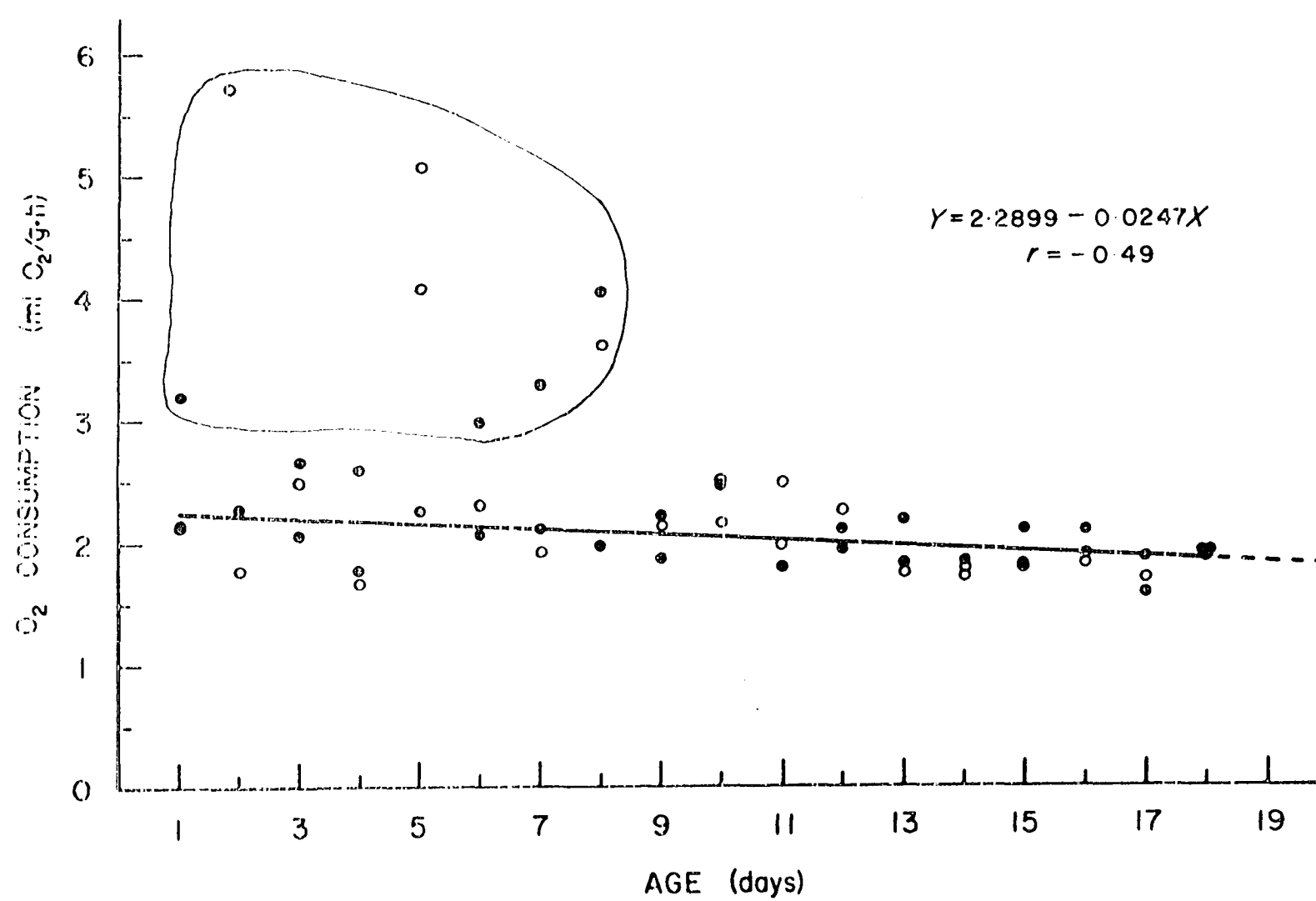
a pattern similar to that for all adult endotherms begins to materialize, *i.e.*, the highest rates of  $O_2$  consumption occur at the higher  $T_a$ 's. Most neonatal cotton rats, however, are unable to maintain a stable rate of  $O_2$  consumption in the 0-5 C range of  $T_a$ 's. It can readily be seen that the capacity for endothermy greatly increases from the third day of life to the tenth day of life (Fig. 12). Oxygen consumption was undetectable at the end of 3.5 hours for 3-day-old neonates tested at 5 C but was found to be 10.3 ml  $O_2$ /g·h for one 10-day-old neonate tested at 5 C. The 10.3 ml  $O_2$ /g·h value is the highest metabolic rate recorded for any neonate tested.

After day 10, a general trend for a reduction of mass specific rate of  $O_2$  consumption at  $T_a$ 's below thermoneutrality can be seen (Fig. 12); *i.e.*, decreases occur in the slopes of the lines which could be fitted to the points representing  $O_2$  consumption at  $T_a$ 's below 35 C. Mass specific rate of  $O_2$  consumption of neonates in thermoneutrality remains relatively unchanged throughout the 1-18 day period although a trend for lower rates with increased age/weight can be seen (Fig. 14). Similar results are obtained if  $O_2$  consumption of animals in thermoneutrality is plotted against body weight (in a log-log plot) rather than age. From day 13 to day 16, a general reduction in variability of rates of  $O_2$  consumption among neonates tested at a given  $T_a$  can be seen (Fig. 12).

#### Total conductance

Plots representing the relationship between total conductance in ml  $O_2$ /g·h·°C can be seen in figure 13. Total conductance is highest

Fig. 14. Relationship of  $O_2$  consumption with age in neonates of Kansas lineage (open circles) and of Texas lineage (closed circles) in thermoneutrality. Points that are encircled represent animals not in a quiescent state and are not included in calculation of the regression line.



( $1.83 \text{ ml O}_2/\text{g}\cdot\text{h}\cdot^\circ\text{C}$ ) in 1-day-old neonates exposed to  $T_a = 35^\circ\text{C}$  and lowest ( $0.65 \text{ ml O}_2/\text{g}\cdot\text{h}\cdot^\circ\text{C}$ ) in 17- and 18-day-old rats exposed to  $T_a = 0^\circ\text{C}$ . The maximum value of total conductance recorded for 18-day-old neonates is approximately 33 % of the maximum value recorded for 1-day-old neonates.

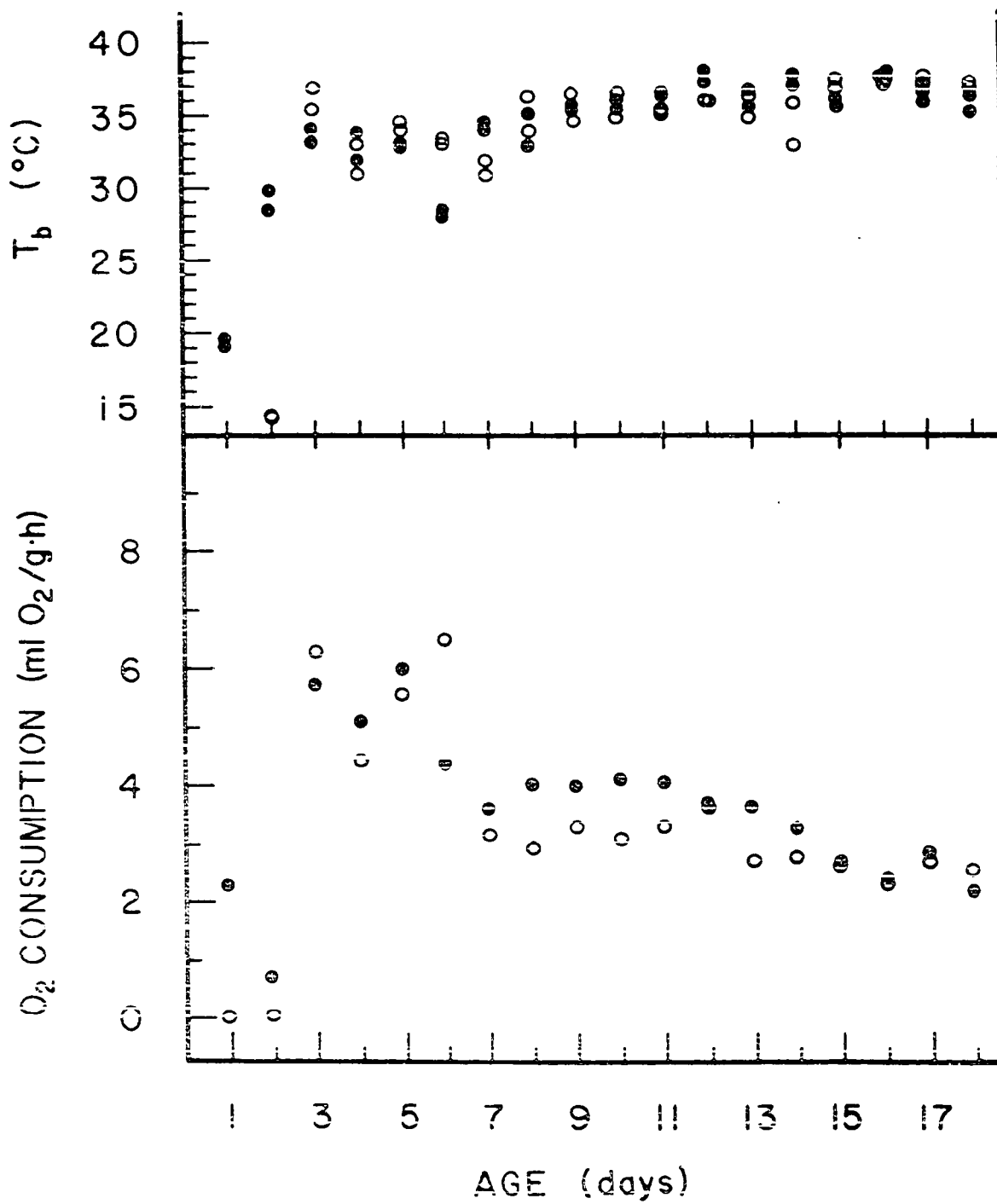
#### Onset of shivering

Nineteen individuals, representing 2 Texas and 2 Kansas litters, were tested daily (or until shivering was noted) to ascertain the age of onset of visible shivering thermogenesis. No pattern of earlier development of shivering in Texas or Kansas neonates could be discerned. The earliest age at which shivering was noted (4 of 19 individuals) was on day 4. Fifteen of 19 neonates tested demonstrated the capability to shiver by day 5. All animals shivered by day 7.

#### Body Temperature and Oxygen Consumption in Litters of Four

Final  $T_b$  in 2 of the 4 siblings and  $\text{O}_2$  consumption of the litter can be seen in figure 15. All litters were tested at  $T_a = 0^\circ\text{C}$ . Only one litter was incapable of surviving the 3.5 hour test period (Kansas: 1-day-olds). Individuals examined for  $T_b$ 's in 1- and 2-day-old Texas litters and the 2-day-old Kansas litter were unable to maintain stable  $T_b$ 's throughout the test period. After day 2, litters become progressively more able to maintain stable  $T_b$ 's throughout the test period with a simultaneous decrease in mass specific rate of  $\text{O}_2$  consumption (Fig. 15). Oxygen consumption is lower in Kansas litters from days 7-14 than in Texas litters. After day 14, rates of  $\text{O}_2$  consumption for

Fig. 15. Relationship of final body temperature and  $O_2$  consumption in litters of 4 Sigmodon hispidus texianus exposed for 3.5 hr to an ambient temperature of 0 C. Animals were in a nest. Open circles represent litters of Kansas origin and solid circles represent litters of Texas origin.



Kansas and Texas litters approximate each other quite closely. Mass specific rate of  $O_2$  consumption for 18-day-old litters in a cotton nest at 0 C is approximately 30 % of the rate for individuals tested at 0 C without access to a nest.

## DISCUSSION

The average sizes of all litters produced during this study by parents of Kansas and Texas origins did not significantly differ;  $6.10 \pm 0.84$  (2SE), range = 2-10 and  $6.53 \pm 0.96$  (2SE), range = 1-12, respectively. Five wild-bred females (i.e., were pregnant upon arrival in the laboratory) from Texas produced most of the larger litters (10-12 individuals/litter) noted in this study. This is unexpected because larger litter sizes are normally associated with increases in latitude (Lord, 1960; Spencer and Steinhoff, 1968; Innes, 1978) and thus, would be expected to be produced by wild-bred females from Kansas (which produced litters 2-3 individuals smaller). Goertz (1965a) and McCleaghan and Gaines (1978) found that the size of the litter is directly correlated with the size of the mother. Data from the present study agree with these findings. Mothers of the larger litters (both Texas and Kansas) were indeed larger than the typical female maintained in the breeding colonies.

Birth weights of young from Kansas and Texas litters are similar to each other (Fig. 10) and are representative of values previously reported for newborn cotton rats (Meyer and Meyer, 1944; Randolph et al., 1977). Weights of the Kansas and Texas neonates become significantly different by day 4. This dissimilarity in individual body weights is probably due to the larger Texas litters. Randolph et al. (1977) reported that while larger litters gained more weight collectively, each individual gained less than individuals from smaller litters. Typically, the lower weights recorded for both Kansas and Texas



neonates were of animals from large litters (7-12 individuals). Also, Texas females appeared to spend less time nursing their young during the day than Kansas females which, assuming the amounts of nocturnal nursing to be similar, could result in a lower growth rate in Texas neonates.

The triphasic growth curve is probably due to a combination of pelage development (insulation), endothermic capability and food consumption. Neonates during the first growth phase (days 1-5) are sparsely furred and have  $T_b$ 's immediately after they are removed from the presence of the mother that average 30-32 C. Neonates in this stage of anatomical development lose much of their heat to the environment (especially when the mother is not in the nest) and consequently, have a suppressed growth rate because of their low  $T_b$ 's (Hill, 1972). Numerous reports have indicated a slowing of growth rate with lowered  $T_b$  in neonatal Peromyscus (Layne, 1968; Hill, 1972), Pipistrellus (Racey, 1969), Myotis (Eisentraut, 1937) and Plecotus (Pearson et al., 1952).

It has been suggested by Balmer and Strobusch (1977) that development of a thick, well-insulating coat of fur in very small newborn mammals (the size of most newborn rodents) is energetically detrimental to the neonate. Balmer and Strobusch (1977) determined that for cylindrical and spherical bodies, a critical body radius exists below which any addition of insulation will increase heat transfer to the environment rather than decrease the flow of heat. Because of this relationship, future studies on development of thermoregulation in small neonates should not look upon sparsely furred newborns as being

at a thermal disadvantage because of their poor degree of insulation.

The second growth phase (days 6-10) is characterized by a more rapid growth rate and probably is tied to increased endothermic capabilities and to further development of the pelage. The increase in amount of insulation of animals the size of 6- to 10-day-olds (11-14 grams) reduces the amount of thermal conductance (as can be seen in figure 13), effectively raising the body temperature (Hissa, 1968). With an increase in body temperature from 30-32 C to 32-34 C, growth rate would be expected to increase which indeed, does occur (Fig. 10).

The third growth phase is the most rapid of the three phases and probably is indicative of a decreased degree of dependence upon the mother for maintenance of body temperature (because of a greater increase in insulation and endothermic capability) and for nourishment (because of the increased ability to consume food other than milk). Body temperatures were typically found to be 35 to 37 C during the third growth phase, regardless of whether the mother was in the nest or not prior to measurement of  $T_b$ . Young during this growth phase were usually observed to be eating crumbs from the food provided for the mother when they were not nursing. This increased food consumption via nursing/eating solid food would provide a maximum amount of energy intake necessary to sustain a relatively high homeothermic  $T_b$  and constant rate of growth. Litters appeared to be weaned between the 18th and 21st day since many litters were observed suckling on day 18 but none were observed on day 21.

Although the sizes of Texas and Kansas neonates are significantly different after day 4, the generally larger size of the Kansas neonate

does not initiate a more rapid rate of attainment of homeothermy or endothermy than in the smaller Texas neonate. Indeed, the responses ( $O_2$  consumption, conductance and  $T_b$ ) of Texas and Kansas individuals at all  $T_a$ 's tested are indistinguishable (Figs. 11, 12, 13 and 14). It is apparent that differences in thermoregulatory abilities that have been shown to exist between adult S. h. texianus of Kansas and Texas lineages (part 1, herein) develop after the 18th day of life.

Animals during the first few days of life are basically poikilothermic in their ability to maintain stable  $T_b$ 's during metabolic determinations. Final  $T_b$ 's were normally within 1 to 2 C of the  $T_a$  at which the animals were exposed. Animals failed to maintain final  $T_b$ 's 1 to 2 C above  $T_a$  only at the lower  $T_a$ 's at which  $T_b$  equaled  $T_a$ . This poikilothermic response is similar to that reported for various species of mice, rats, hamsters, lemmings, voles and ground squirrels (see Table 4). The tendency for young neonates to resemble poikilothermic animals in their thermoregulatory abilities is advantageous in terms of energetic costs. Kleiber (1932) has shown that the cost of being homeothermic increases geometrically as body mass decreases. For a young neonate to maintain its  $T_b$  at a level similar to older neonates or adults would entail a tremendous metabolic expense, leaving less energy for growth and development (McManus, 1971). By remaining primarily dependent upon maternal heat for maintenance of a stable  $T_b$  before insulatory features are more adequately developed (by days 7-10), neonates can channel a larger portion of their energy intake into growth and development. The development of insulation can be

gauged by the decrease in total conductance (Hissa, 1968), which at  $T_a = 35^\circ\text{C}$  decreases by as much as 66 % from day 1 to day 13 (Fig. 13).

All newborn animals tested at various  $T_a$ 's exhibited some capability for endothermy which indicates that the thermoregulatory control system is at least partially functional at birth, i.e., the neonate is capable of sensing  $T_b$ , integrating sensory input and effecting thermogenic processes. Similar responses in newborn neonates have been reported for other small mammals such as Lemmus lemmus (Hissa, 1964), Rousettus aegyptiacus (Noll, 1979), Galago senegalensis moholi (Dobler, 1976), white laboratory rats (Gelineo and Gelineo, 1951; Taylor, 1960), domestic rabbits (Dawes and Mestyan, 1963; Hull, 1965), guinea pigs (Dawes and Mestyan, 1963; Bruck and Wunnenberg, 1965) and domestic kitten (Hull, 1965). The age at which the first metabolic response occurs in white mice varies with the strain of mice studied. Numerous studies have been conducted on white mice of which Cassin (1963), Pichotka (1964), Lagerspetz (1966) and Chew and Spencer (1967) have reported metabolic responses to cold in 1-day-old neonates. Chew and Spencer (1967) indicate that in general, newborns weighing less than 4 grams will exhibit a response. Since newborn of S. hispidus average 6.30 and 6.19 grams in Kansas and Texas litters, respectively, the metabolic response exhibited by newborns in this study is not unexpected.

As the neonates mature (days 1-7), an increase in endothermic capability can be seen in figure 12. Nonshivering thermogenesis (NST) is probably the primary process responsible for thermogenesis in the neonate during the first few days of life (Hull and Segall, 1965a; Bruck and Wunnenberg, 1966). The importance of NST is succeeded by shivering

thermogenesis (ST) as the neonate matures (Bruck and Wunnenberg, 1965, 1966; Hissa, 1968; Arjamaa and Lagerspetz, 1979). The age at which NST is replaced by ST is dependent upon the degree of anatomical development at birth (Jansky, 1973) and has been closely correlated with postnatal maturation of the nervous system (Hahn et al., 1956; Hissa, 1968; Lapointe and Nosal, 1979). The earliest age for which visible shivering was noted in neonatal cotton rats was day 4. All neonates tested shivered by day 7. Onset of visible ST is earlier in neonatal cotton rats than that reported for other similarly sized rodents. Ages reported for onset of visible ST range between 9-12 days for laboratory rats (Gulick, 1937) although Taylor (1960) did not note visible ST in white rats until day 19. The onset of visible ST has been reported to occur at 7-8 days in Lemmus lemmus (Hissa, 1964), 10-11 days in golden hamsters (Hissa and Lagerspetz, 1964), 18-19 days in Baiomys taylori, 14 days in Perognathus longimembris, 9-18 days in Peromyscus maniculatus, 9-11 days in Mus musculus (Chew and Spencer, 1967) and 10-12 days in Peromyscus leucopus (Hill, 1976). Maxwell and Morton (1975) reported onset of ST in Spermophilus beeldingi beeldingi (a hibernator) to occur by the 15th day whereas onset of ST occurs by day 25 in Ammospermophilus leucurus leucurus (a nonhibernator). Maxwell and Morton (1975) hypothesized that the earlier attainment of thermoregulatory ability in the hibernator was adaptive in that it enabled early emergence from the natal burrow. Early emergence would permit additional time to attain a sufficient body weight to survive the oncoming hibernation season. Early attainment of thermoregulatory abilities would be adaptive to survival of neonatal S. hispidus. High rates of

predation on the nests of cotton rats have been reported by Selander and Walker (1955). The sooner the young can leave the nest the less chance there is for an entire litter being destroyed by predation. Odum (1955) and Goertz (1965a) have reported captures away from the nest of cotton rats estimated to be as young as 4 days of age, although according to the age-weight relationships determined in the present study the age of these animals would be closer to 7 days of age. Nevertheless, the early age of onset of visible ST in S. hispidus corresponds quite well with the relatively advanced stage of anatomical development at birth (Randolph et al., 1977) as suggested by Jansky (1973).

Thermoregulatory abilities of animals 1-7 days of age appear to be more dependent upon age rather than weight. Smaller, older animals possess a greater ability to maintain a higher final  $T_b$  than younger, larger animals. This occurrence indicates that during the first week of life, body size is less important for maintenance of homeothermy than the degree of maturation of the thermoregulatory control system. One- to 5-day-olds could be chilled to final  $T_b$ 's close to 5 C without becoming comatose. Individuals older than five days were incapable of being chilled to similar final  $T_b$ 's without becoming comatose. Similar instances have been reported for various species of rodents (Adolph, 1951; Fitzgerald, 1955; Hill, 1976). Older neonates apparently have an established set point (which increases with age until adulthood is reached) for the lowest  $T_b$  at which they can survive (Adolph, 1951).

After day 7, neonatal S. hispidus develop an increased ability with age/weight to thermoregulate at low  $T_a$ 's (Figs. 11, 12 and 13).

Mass specific rates of  $O_2$  consumption at  $T_a$ 's below thermoneutrality initially increase with age until about day 10 (approximately 15 grams) after which a decrease occurs. A period of increasing metabolic capacity per unit of body weight during the postnatal growth period has been reported for Lemmus lemmus (Hissa, 1964) and the golden hamster (Hissa, 1968) until weights of approximately 18 and 12 grams are attained, respectively. Chew and Spencer (1967) also reported increases in mass specific rates of metabolism with increasing weight in Baiomys taylori, Perognathus longimembris, Peromyscus maniculatus and Mus musculus. However, decreases in rate of  $O_2$  consumption did not occur in those species until adult weights were reached. Mass specific rates of  $O_2$  consumption of S. hispidus in thermoneutrality tend to decrease somewhat with increasing age (Fig. 14). This correlation, however, is poorly defined, e.g., the rates of 18-day-olds are higher than approximately 50 % of the values determined for younger, smaller individuals. The decreases in mass specific metabolic rates below thermoneutrality after day 10 are probably due to the reduced levels of total conductance. Indeed, between days 10-18 metabolic rates will cease to decrease (Fig. 12) and remain relatively constant at the same age- $T_a$  combination at which total conductances cease to decrease and remain relatively constant (Fig. 13). This relationship clearly illustrates the ability of neonates to balance heat generation with heat loss in order to maintain a relatively homeothermic  $T_b$  at increasingly lower  $T_a$ 's (Fig. 11). By day 13 young of S. hispidus are essentially homeothermic; average  $T_b$  is approximately 35-36 C at all  $T_a$ 's tested (Fig. 11). From day 13 to day 18 changes in thermoregulatory responses are basically

refinements of the pattern that is established by day 13 and represent what Hahn et al. (1956) describe as "the formation of new relationships between the physical and chemical component of thermoregulation" (i.e., increased neurological integration of the existing thermoregulatory mechanisms along with a change in the regulation of the metabolism). Future studies are planned to examine the continued development of thermoregulatory abilities and processes of Kansas and Texas animals until the adult characteristics are achieved.

Since neonatal cotton rats are typically found in nature as litters in a nest, a look at thermoregulatory abilities of litters of cotton rats is of interest. Litters of 4 were subjected to a  $T_a$  of 0 C for 3.5 hours. Responses of the litters can be seen in figure 15. It is apparent that huddling, combined with the additional insulation of a nest, generates metabolic savings up to 67 % of the cost of thermoregulation of the individual at 0 C. By day 3, animals in a litter are capable of maintaining final  $T_b$ 's above 30 C. No doubt, abilities of litters to thermoregulate would be much greater at warmer  $T_a$ 's. The data for  $O_2$  consumption in 7- to 14-day-old litters suggest different thermoregulatory abilities in Kansas and Texas litters. Most likely these differences can be dismissed as differences due to activity of the young. In several instances 1 or 2 Texas neonates were noted to have burrowed through the cotton nest and were separated from the others. This separation would have the effect of raising the apparent rate of  $O_2$  consumption for the litter. Rates of  $O_2$  consumption are very similar in Kansas and Texas litters 15-18 days of age.



Neither litters of cotton rats nor individual neonates are ever subjected to environmental temperatures in nature close to the low  $T_a$ 's used in the present study. Consequently, thermoregulatory abilities determined for the neonates in this study reflect responses to unrealistic situations for the young of S. hispidus. Information gathered in this study, however, suggests a rapid rate of development of thermoregulatory self-sufficiency in young S. hispidus. This self-sufficiency would permit early dispersal from the nest (and nest predation), thereby increasing the chance for species survival.

## SUMMARY AND DISCUSSION

Data presented in the previous two sections indicate that differences in the thermoregulatory abilities of Sigmodon hispidus texianus of Kansas and Texas ancestry do not appear until sometime between the 18th day of life and adulthood.

Kansas neonates are significantly larger than Texas neonates after the fourth day of life. The significantly larger size of Kansas neonates after day 4 does not contribute to a more rapid attainment of homeothermy than that of Texas neonates. Indeed, thermoregulatory responses ( $O_2$  consumption, total conductance, onset of visible shivering, body temperature) of Kansas and Texas neonates exposed to ambient temperatures of 0-35 C are indistinguishable. Neonatal S. hispidus achieve homeothermy at ambient temperatures between 0-35 C by the 13th day of life, which is sooner than the average age for attainment of homeothermy in other species of rodents (18 days). The relatively rapid rate of development of thermoregulation in the young of S. hispidus probably is adaptive in that it would permit early dispersal (at ages as young as 4-7 days) of young from the nest. Nests of S. hispidus have been reported to be subjected to heavy predation; thus, early dispersal of the young would decrease the possibility of an entire litter being destroyed by predation.

By the time adulthood is reached significant differences in thermoregulatory abilities do exist between cotton rats of Kansas and Texas lineages. Basal metabolism in Kansas animals is significantly lower than that in Texas animals. This reduction is probably in

response to a greater need for water conservation in the drier areas of Kansas. Similar instances have been shown for other rodents inhabiting xeric areas of North America. Body temperatures of Kansas and Texas animals, however, are similar (approximately 38.1 C) at ambient temperatures between 0-35 C. Kansas animals are capable of maintaining a body temperature similar to that of Texas animals because of a significant reduction in the rate of thermal conductance (both total and dry). Because of the significant reduction in dry conductance in Kansas animals, evaporative cooling at high ambient temperatures is of greater importance to Kansas animals than to Texas animals. This difference, however, is probably relatively unimportant under natural conditions since S. hispidus probably avoids exposure to high environmental temperatures.

In the process of northward migration into drier and cooler regions of the Great Plains, natural selection has occurred in S. h. texianus. Individuals possessing the traits for lowered basal metabolism and reduced total and dry conductances have been selected for by evolutionary processes. These traits enable animals to conserve water which may be in short supply during the drier and warmer periods of the year while maintaining body temperature at a level similar to that found in animals at the southern end of the distribution of the subspecies.

These adaptations have secondarily permitted animals in the northern regions of the distribution to more efficiently thermoregulate at low environmental temperatures during winter. The reduction in total and dry conductances enables Kansas animals to conserve

significantly more endogenous heat than Texas animals and thus, maintain normothermic body temperatures at a lower metabolic cost. At an ambient temperature of 0 C, Kansas animals are able to maintain similar body temperatures to those of Texas animals for only 88 % of the metabolic cost, and this savings increases as ambient temperature approaches thermoneutrality. No doubt a metabolic savings of 12 % (or more) prorated over an entire winter season in Kansas may be of extreme importance for survival, especially when food and water may be in short supply and difficult to procure.

Winters in northern Kansas are very harsh compared to winters in Texas. Populations of S. h. texianus in northern Kansas typically undergo large reductions in numbers or total local extinction due to lack of sufficient food availability and cold environmental temperatures. It is my belief that the original adaptive advantages of reductions in basal metabolism and thermal conductances for conservation of water probably are overshadowed in the more northern populations by the advantages of heat conservation and food conservation during winter. Such abilities would permit animals to withstand periods of very cold temperatures during winter (either by foraging for needed food resources during these times or surviving longer periods of cold weather starvation between feedings), thereby ensuring survival of the species in the more northern latitudes.

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